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THE STRUCTURE OF THE SPIRACULAR GILL OF THE GENUS *LIPSOTHRIX* (TIPULIDAE), WITH SOME OBSERVATIONS ON THE LIVING EPITHELIUM ISOLATED IN THE GILL AT THE PUPA-ADULT MOULT.

By H. E. HINTON, Ph.D., F.R.E.S.

(Department of Zoology, University of Bristol.)

1. INTRODUCTION.

THE structures that have been called spiracular gills (Hinton, 1953) are all modifications of the spiracle, or the integument of the body wall immediately adjoining the spiracle, or both. To understand the full significance of spiracular gills, it is necessary to consider them not merely as structures adapted for under-water respiration, but as structures adapted both for extraction of oxygen from the water, and for atmospheric respiration. In water they provide a relatively enormous surface area for diffusion, and the structure of their walls is such as to prevent their collapse under the hydrostatic pressures to which they are normally subject. Figures are not available to show in any one species the proportion of the oxygen demands satisfied by diffusion through the body-wall cuticle and the gill, but in many species the total surface area of the gill is such as we may suppose that no limit is set to the impermeability of the body-wall cuticle. When the pupa or pharate adult¹ is out of water, the enormous surface area of the gill does not involve the animal in water loss over such an area, since the connection between the lumen of the gill and the internal tissues of the insect is restricted to a surface hardly, if at all, greater than that of the spiracles of terrestrial insects. Thus, a spiracular gill not only provides an enormous surface area for the extraction of oxygen from the ambient water, but in the air the total surface area for humidity exchanges between the saturated air in the tracheae and the drier air outside is about as restricted as in any terrestrial insect with normally formed spiracles.

Spiracular gills are thus an adaptation that enables the immobile, or relatively immobile, pupa or pharate adult of some insects to meet the contradictory demands presented to them by environments that are alternately dry and flooded. It is, therefore, no accident that spiracular gills are largely confined to the pupae of groups that inhabit rapidly flowing or torrential streams, since one of the most characteristic features of such streams is the rapid fluctuation of the water level. Spiracular gills are known to occur in the pupae of the following stream forms: Psephenidae (*Psephenoides*), Tipulidae (*Taphrophila*), Chironomidae, Blepharoceridae, Deuterophlebiidae, Simuliidae, and Empididae (Hemerodromiinae). Multi-branched spiracular gills are present in most Chironomidae whether they be stream forms or not, and unbranched spiracular gills are present in some intertidal Clunioninae. Most of the Chironomidae that do not live

¹ In order to avoid circumlocution, the term "pharate" has been proposed (Hinton, 1946) to designate the phase of an instar or stage which is enclosed within the cuticle of the previous instar or stage, e.g. when the insect is in the pharate adult phase, the pupa-adult moult has taken place, but the adult has not shed the pupal cuticle, which is now only mechanically connected to the living insect.

in streams live in shallow bodies of water. Here, as in streams, they are frequently exposed to alternate flooding and drying. In addition, an intertidal Tipulid (*Geranomyia*), which is exposed to alternate flooding and drying, has spiracular gills. Most of the descriptions of the spiracular gills of these species are of a general character, but those of *Simulium* (Taylor, 1902) and *Psephenoides* (Hinton, 1947) have been described in detail.

The evolution of spiracular gills is not, of course, the only way in which insects solve the very special problems that accompany the invasion of aquatic environments that may suddenly dry up completely for prolonged periods. How they do so is determined, on the one hand by their previous history, and on the other by the specific attributes of the particular environment that is alternately dry and flooded. Perhaps the most unusual adaptation to such environments is the capacity to tolerate complete dehydration of the tissues, e.g., the larva of the Chironomid *Polypedilum vanderplanki* Hint. (Hinton, 1951) and that of an African Ceratopogonid, an account of which will be published later. Other ways in which the difficulties of such environments have been overcome by different insects are reviewed by Hinton (1953).

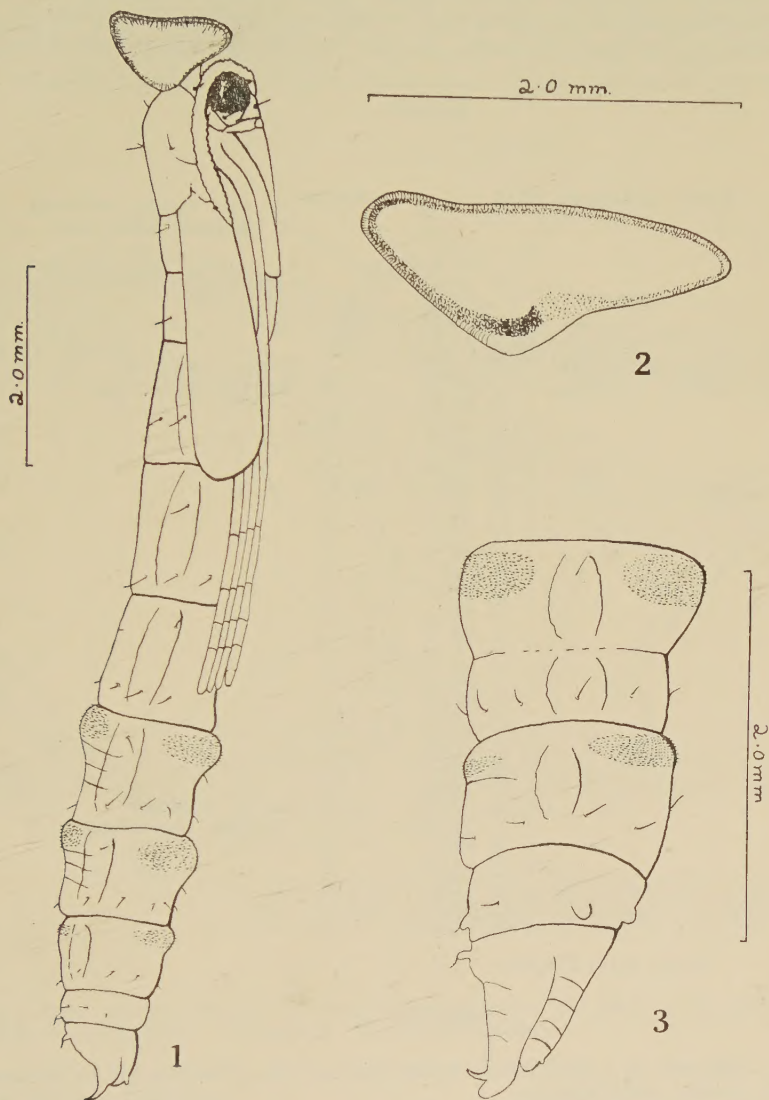
The spiracular gills of *Lipsothrix* (Eriopterini) are more complex than those of any other insect so far described. They are also of especial interest because at the pupa-adult moult about 1100 epidermal cells are isolated in the cavities of each of the two gills, and cease to have any connection with the tissues of the living insect. This phenomenon appears to be without parallel among insects. For reasons given below, it is suggested that these cells may function in healing wounds to the spiracular gill of the pupa after the insect has become an adult, but while it still uses the pupal gill for respiration, although only mechanically connected to it.

The account given below is based on *Lipsothrix remota* Walk., but the spiracular gills of *L. nervosa* Edwards are identical in all essentials, except that on the outer wall the more or less straight aeropyles are much longer, and there is no reticulate network. The larvae of both species mine in stems and trunks of oak lying on the banks of streams in Somerset and Gloucestershire. They have usually been found in stems and trunks above the level of the water, but *L. remota* has been found on several occasions in the submerged parts of oak logs. Most have been found sufficiently close to the water so that any appreciable flooding of the stream would submerge or partly submerge the wood in which they were feeding. Larvae and pharate adults of *L. remota* survived for many days when placed in artificially aerated water from which air bubbles were excluded. Submerged larvae were able to pupate. The larval cuticle can be shed beneath the water. The adult does not appear to be able to shed the pupal cuticle beneath the water, and on one occasion a pharate adult was kept submerged for eight days. *Taphrophila*, the other freshwater Tipulid with spiracular gills, can shed the pupal cuticle both in and out of the water (Hinton, 1950), as can all other stream insects with spiracular gills that have been tested. *Lipsothrix*, however, is, with the exception of some Chironomids, by far the least aquatic of the insects with spiracular gills. It may be noted here that the intertidal *Geranomyia* is only known to shed its pupal cuticle when the tide has fallen sufficiently to leave it exposed.²

² The Japanese intertidal species of *Dicranomyia* also shed the pupal cuticle only when exposed above water (Tokunaga, 1933).

2. GENERAL STRUCTURE OF THE SPIRACULAR GILL.

The general appearance of the spiracular gill is shown in figs. 1-2, and the terminology used in this paper is explained in fig. 4. When the pupa is placed



FIGS. 1-3.—Pupa. (1) Lateral view of right side of male pupa. (2) Inner view of a prothoracic spiracular gill. (3) Lateral view of the right side of the end of the abdomen of a female pupa.

with its dorsal surface uppermost and its head directed away from the observer, the top of the gill is its dorsal side, the bottom of the gill is its ventral side, the surface nearest the median line of the pupa is its inner external wall, and the

wall furthest from the median line is its outer external wall. The base of the gill is its junction with the body. Each gill is curved outwards in the middle, but both dorsally and ventrally each curves inwards and more or less meets, or even overlaps, its fellow of the opposite side. Thus, from a frontal view the two spiracular gills form a deep and broadly oval hollow, the bottom of which is formed by the top of the head. In this way the delicate cuticle of the inner

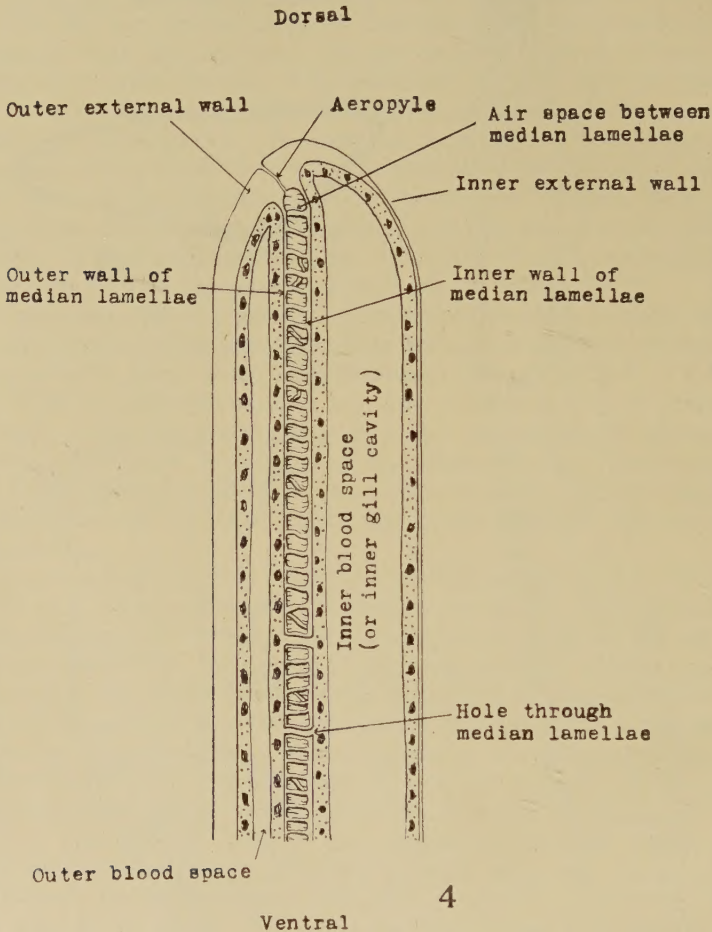
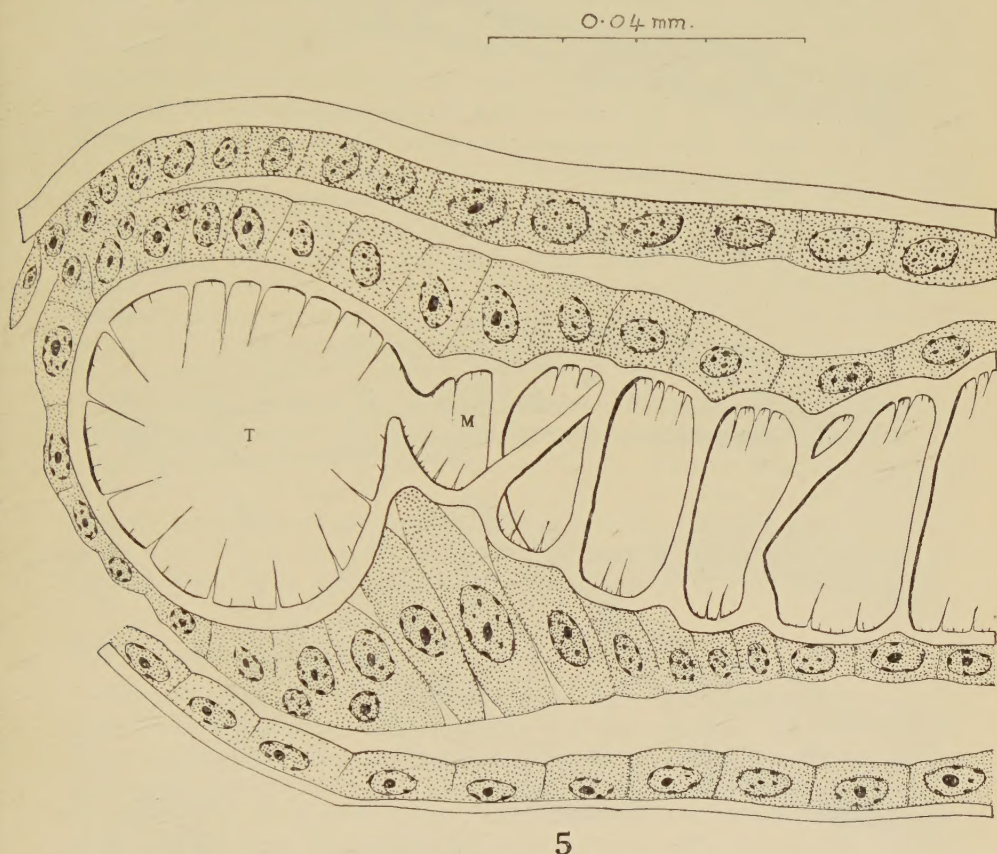


FIG. 4.—Diagram of a longitudinal section through the spiracular gill to illustrate the terminology used in the text.

external walls is partly protected from abrasion which might result from the movements of the pharate adult in the pupal cell or in the gallery in the wood. The size of the spiracular gill in relation to the size of the pupa is shown in fig. 1. Variations in the size of the spiracular gills relative to the size of the pupae are chiefly due to differences in the contraction of the body of the pupa.

The trachea that enters each spiracular gill is anchored to the cuticle of the

body wall of the pupa along a narrow line proximal to the base of the gill. Such points of attachment are common in the Tipulidae, where, in some species, e.g. *Crunobia litoralis* Meig., the trachea proximal to the respiratory horn is anchored to the body wall by a large and conspicuous apodeme. These structures may be called "tracheal anchors." They restrict movements of the main trachea entering the respiratory horn or spiracular gill during the pharate adult phase, when the trachea is no longer held in place by its tissue attachments.



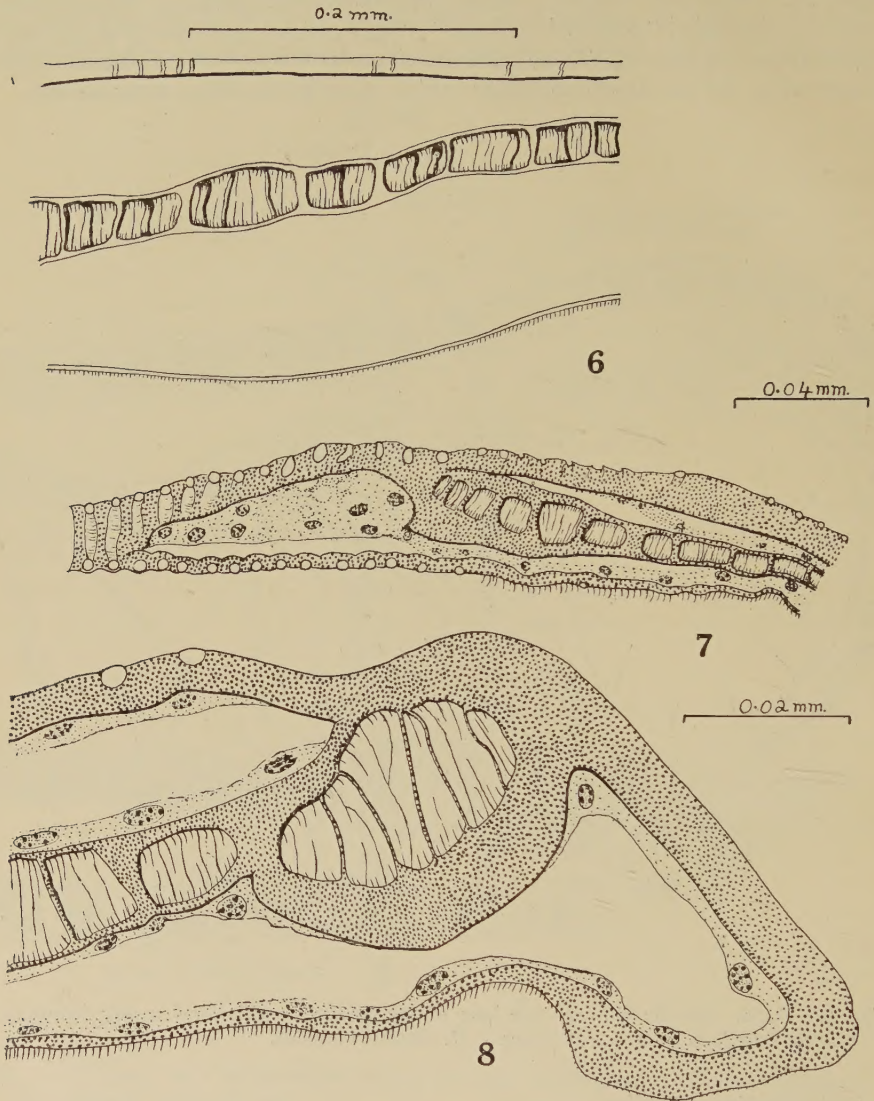
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FIG. 5.—Pupa. Section through the base of the spiracular gill about a day before the larval cuticle is shed. *T*, trachea; *M*, median lamellae.

(a) *The Median Lamellae.*

The median lamellae are two separate sheets of cuticle that are fused to the cuticle of the outer external wall of the spiracular gill near its rim. They enclose an air space that is continuous with that enclosed by the tracheae. The epithelium that secretes the median lamellae is continuous with the tracheal epithelium, as clearly shown in fig. 5; and the cuticle of the median lamellae is continuous with the cuticular walls of the trachea that extends into the spiracular gill. The two median lamellae are separated everywhere by about 15–30 μ .

A series of cuticular columns (figs. 5-9, 13) prevent movements of the lamellae with respect to each other. They also presumably serve to maintain the integrity of the air space when the gill is under sufficient hydrostatic pressure to have



FIGS. 6-8.—Spiracular gill of the pupa. (6) Transverse section through the middle of a gill treated with KOH. (7) A section through the junction of the median lamellae with the outer external wall of the gill. (8) A similar section of another part of the rim of the gill.

the thin inner external wall pressed inwards. Numerous very fine cuticular processes of variable length extend inwards from both walls of the median lamellae. The possible function of these processes is not very evident. They

are nothing like as dense as the processes that are usually thought to establish a humidity gradient in the spiracles of some insects. It may be that they function, together with the stout cuticular columns, to prevent particles of dust and other debris from entering the tracheae should the gill be broken.

The median lamellae are pierced by a number of holes (fig. 14) which effect the continuity of the tissues in the outer and inner cavities of the gill. But for these holes the tissues of the inner and outer cavities of the gill would be completely separated when the basal occluding membrane was secreted at the pupa-adult moult. In many preparations nuclei of the epithelium of either the inner or outer median lamellae were found over some of the holes. This suggests that after the holes are formed they may be partly or entirely occluded by movements of the epithelia in question, and that through such holes there is no free movement of blood between inner and outer gill cavities. In gills of equal size the number of holes varies greatly. The numbers in the right and left gills of four specimens were as follows: 44 : 46, 49 : 34, 48 : 56, and 120 : 75. The holes are usually broadly oval or nearly circular, and most are between 15 and 25μ broad. Much smaller and much larger holes are not uncommon. The largest hole measured $75 \times 20\mu$. The holes are irregularly distributed in the median lamellae, but about two or three times as many are usually present in the ventral half of the gill. Both large and small holes are particularly easy to see when the gill is dried.

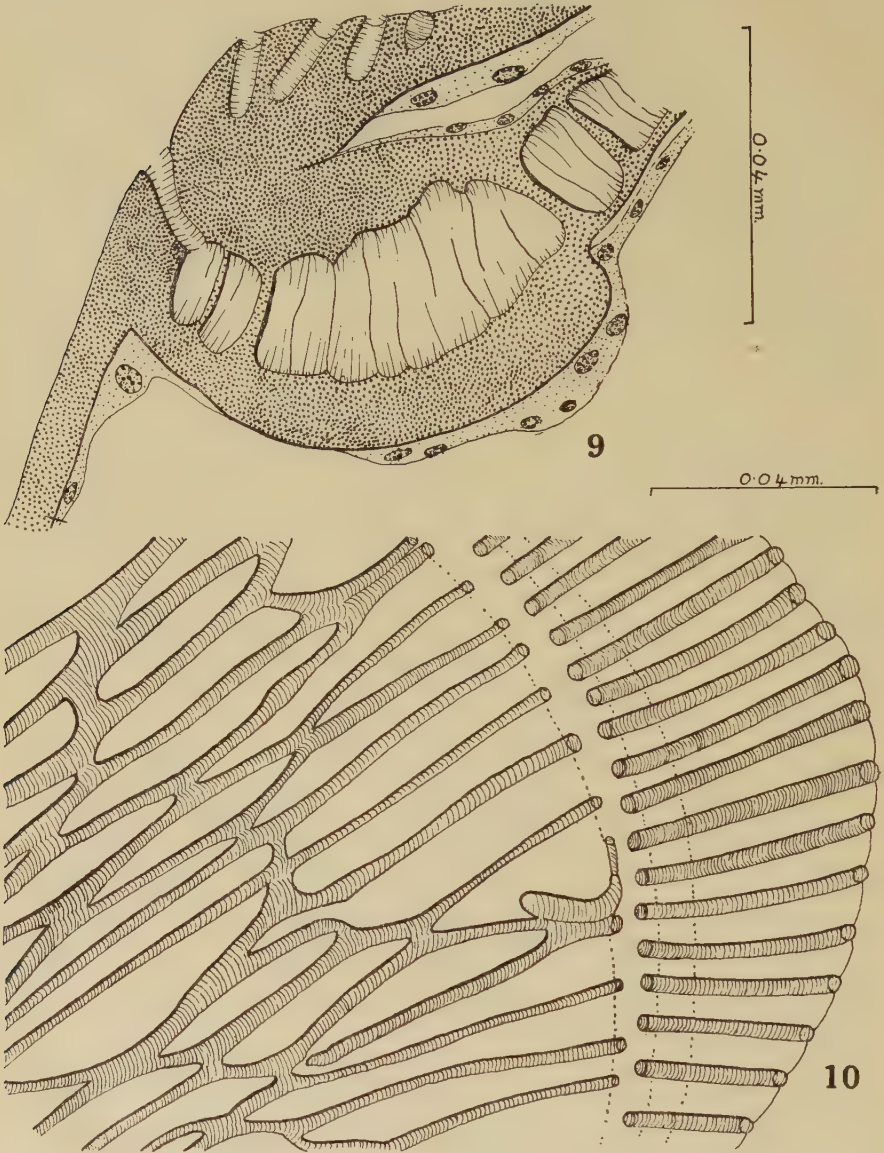
The lumen of the median lamellae effects the continuity of the lumen of the tracheae with the system of superficial air channels or aeropyles. It may also be supposed that whenever a gradient is established between the oxygen tension in the lumen of the lamellae and that in the ambient water, oxygen will diffuse through the relatively enormous surface area of the very thin and soft cuticle of the inner external wall of the gill into the inner gill cavity, and then into the lumen of the median lamellae.

(b) *The System of Superficial Air Channels.*

The outer surface of the spiracular gill, except for a ventral area near its base, is covered with a reticulate network of superficial air channels (fig. 12). These air channels are usually $5-8\mu$ broad, but, where two or more join, a channel 12μ or slightly broader may be formed. This network of air channels is drained by a series of more or less straight and parallel channels, about $40-80\mu$ long, near the rim of the gill (fig. 10). On the outer surface of the gill, near the rim, there is a very lightly impressed line. This line is usually about 50μ from the rim, but it may be as much as 125μ from the rim near the dorsal base of the gill. It lies on the darkly pigmented band that parallels the rim and marks the junction of the median lamellae with the outer wall of the gill. At the lightly impressed line, the more or less straight air channels that drain the reticulate network dip almost at right angles into the cuticle. They extend through the cuticle for a variable distance, usually about 20μ or so, to empty into the air space enclosed by the median lamellae (fig. 9). The very regular series of channels that drain the reticulate network are present right around the gill almost to its base on the dorsal side, but end some little distance from its base on the ventral side. It should be noted that there is a single system of air channels on the outer surface, and that each of the channels that drains it

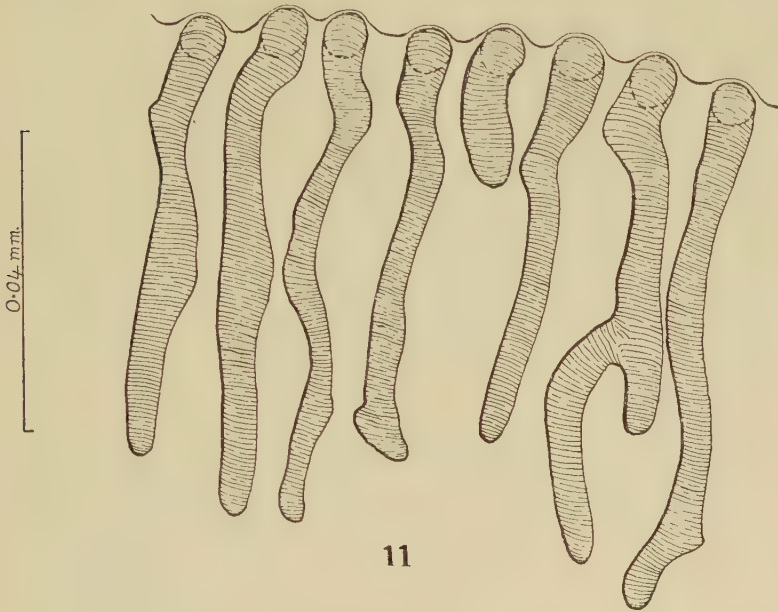
communicates through the network with every other draining channel. In a gill 1.9×0.85 mm. there were 446 of the channels draining the network.

On the opposed or distal side of the lightly impressed line near the rim of the spiracular gill there is a similar series of channels (fig. 10). These extend over

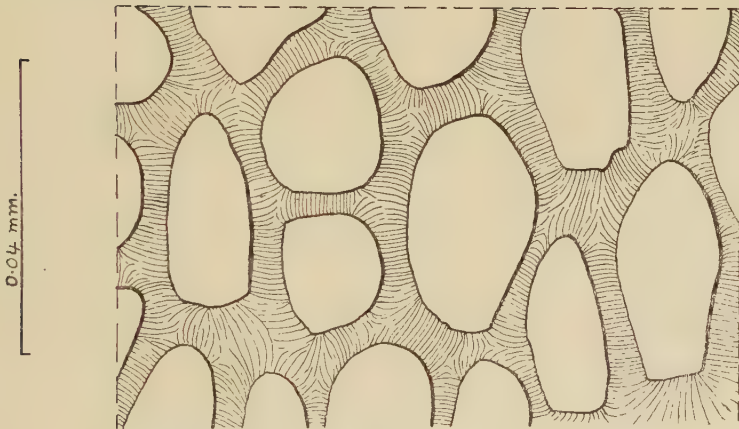


FIGS. 9-10.—Spiracular gill of the pupa. (9) Section through the junction of the median lamellae with the outer external wall of the gill showing an aeropyle communicating with the air space enclosed by the median lamellae. (10) Surface view of the superficial air channels or aeropyles near the rim of the spiracular gill.

the rim and down on the inner side of the gill. On the inner side of the gill they are found only on the hard and thick cuticle near the rim and never on the very thin cuticle. On the inner side they vary from 20 to about 80μ in length. They are occasionally branched (fig. 11), but they end blindly in the



11



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FIGS. 11-12.—Spiracular gill of the pupa. (11) Aeropyle system on hard and thick cuticle of the inner external wall of the spiracular gill. (12) A part of the reticulate network of aeropyles on the middle of the outer external wall of the spiracular gill.

cuticle. A network of channels is never present on the outer surface distal to the above-mentioned lightly impressed line, or on the inner side of the gill. At the lightly impressed line, these channels dip into the cuticle more or less at right angles to the plane of the surface, and communicate with the air space

enclosed by the median lamellae, just as do the channels that drain the reticulate network.

Over all of the superficial channels, both of the network and the draining system, there are very fine and regular cuticular rods. These rods appear to support a very delicate membrane. When the gill is dry and seen by reflected light, there appears to be no doubt about the existence of a delicate membrane, but the rods are so close together that they may give the appearance of a continuous sheet. In oblique or transverse sections the superficial air channels appear to be covered by a membrane, but it is not beyond the bounds of possibility that in each instance it is one of the rods that appears to be the edge of the membrane. In experiments with oils of different mobilities, penetration of the air channels occurred more quickly than I would have supposed possible if they were, in fact, covered by a continuous membrane.

Air channels somewhat comparable to those of the spiracular gill of the pupa of *Lipsothrix* form part of the respiratory system of certain insect eggs. For such channels in insect eggs the name "pseudomicropyles" was proposed (Beament, 1947). A more suitable name for these minute air channels in eggs and pupae is "aeromicropyles" or, more simply, "aeropyles."

(c) *The Basal Occluding Membrane.*

A section through the base of the gill in the pupal stage, *sensu stricto*, about a day before the larval cuticle is shed, is shown in fig. 5. At this time the outer and inner gill cavities are continuous with the haemocoel, and there is no sign of the basal occluding membrane, which is always present in the pharate adult phase (fig. 13).

It would seem that the basal occluding membrane that cuts off the gill cavities from the haemocoel, and therefore isolates the tissues in the gill from the living animal, is secreted at the pupa-adult moult. Its formation has not been directly observed, nor, indeed, has the precise moment of the pupa-adult moult been determined. However, the occluding membrane is always absent in the pupal stage well before the larval cuticle is shed, and it is always present in the pharate adult stage. From cultures and from the field a total of 36 pharate adults were collected. No pupae (*s. str.*) out of the larval cuticle were found at any time. This raises the question of the duration of the pupal stage after the larval cuticle is shed. Since some of the pharate adults from my cultures were preserved well within 12 hours of the time the larval cuticle was shed, it is clear that the duration of the pupal stage after the larval cuticle is shed must be less than 12 hours. It therefore follows that the greater part of the pupal stage, if not all of it, is passed within the larval cuticle.

My material of *Lipsothrix* is unfortunately inadequate to determine the exact duration of the pupal stage. I have, however, a specimen of another Tipulid, *Crunobia litoralis* Meig. (Pedicini), preserved at the moment when the larval cuticle was half shed. Sections through the tarsi of this specimen show that the epithelium is no longer connected to the cuticle. The pupal cuticle of the wing is also unconnected to the epithelium. Although the space between the epithelium of the tarsi and the cuticle may be the result of contraction during dehydration, it is difficult to see why in that case fragments of the epithelium did not remain attached to portions of the cuticle. The free cuticle over the wing epithelium is, however, convincing evidence that at least the initial stages

of the pupa-adult moult have already been completed at the time that the larval cuticle is shed. It thus follows that at any rate in some Diptera, the functions subserved by the pupal stage can be completed entirely within the larval cuticle

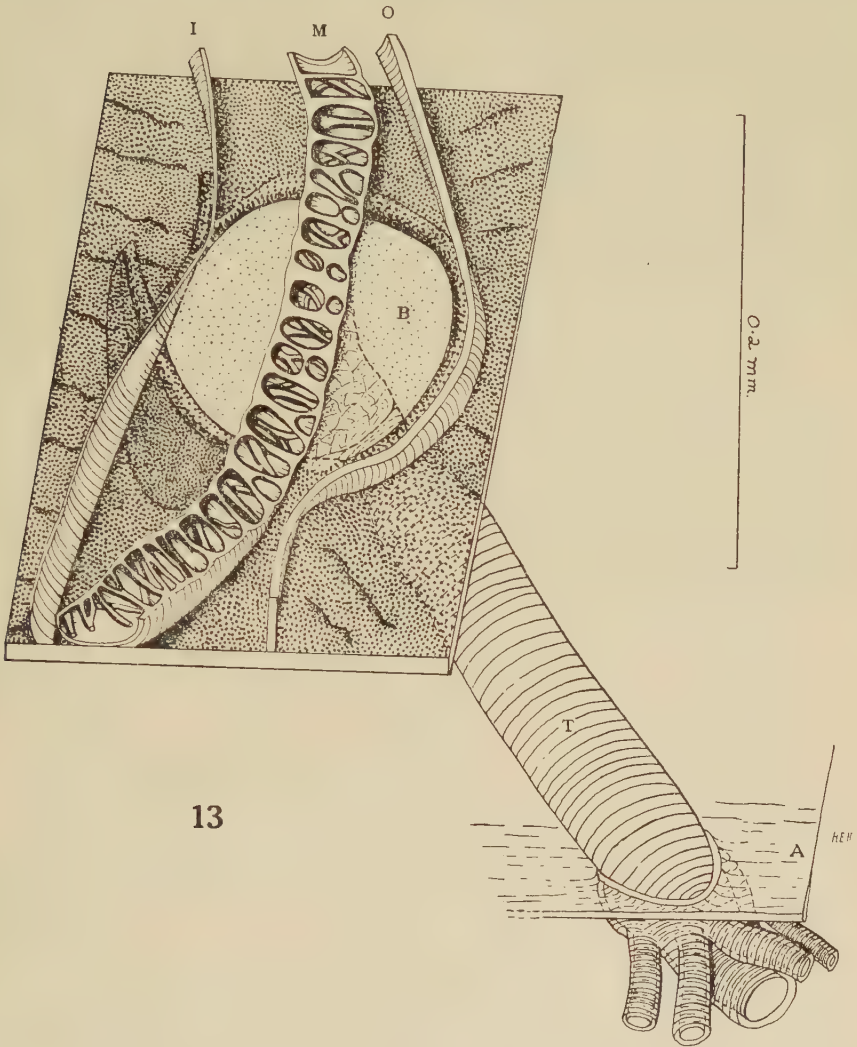
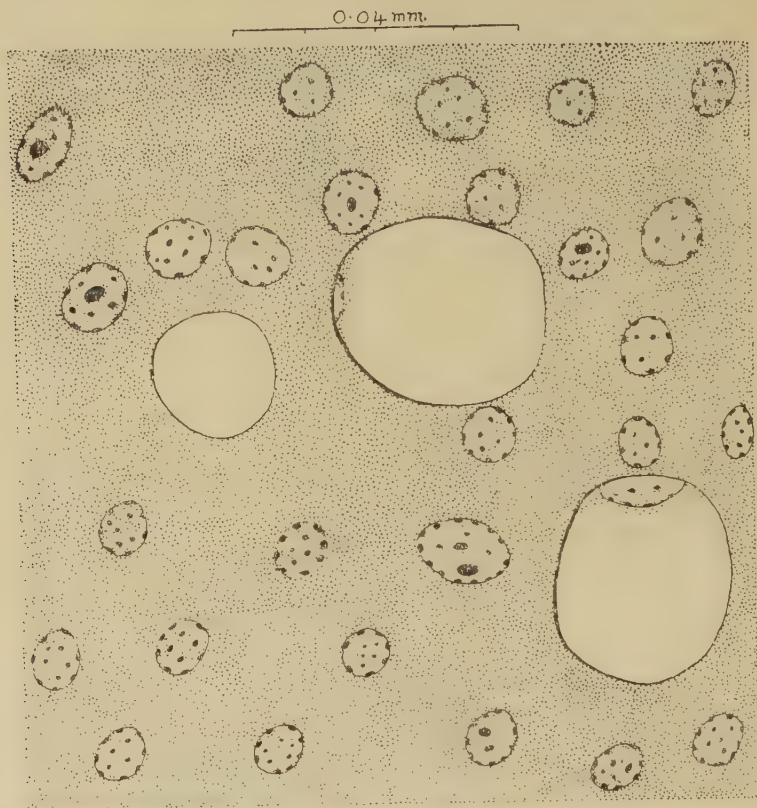


FIG. 13.—Spiracular gill in the pharate adult stage. *A*, Cuticle of body-wall of adult; *B*, basal occluding membrane; *I*, inner external wall of gill; *M*, median lamellae; *O*, outer external wall of gill; *T*, trachea.

and that the spatial requirements of the pupal stage (see Hinton, 1948) can be satisfied by stretching the larval cuticle. In *Crunobia litoralis* the pupal stage is more or less equivalent to the stage usually known by entomologists as the "prepupal stage" or the "prepupal larva".

3. *Tissues Isolated in the Spiracular Gill at the Pupa-adult Moulting.*

When the basal occluding membrane is formed at the pupa-adult moult a large number of living cells are isolated in the outer and inner gill cavities. These are the cells of the epithelia of the inner and outer median lamellae and the inner and outer walls of the gill. At the same time, the blood contained in the inner and outer gill cavities is isolated from the living animal. This blood



14

FIG. 14.—Spiracular gill. Epithelium of outer wall of median lamellae approximately 24 hours after the pupal cuticle was shed by the adult. The three holes extend through both walls of the median lamellae and effect the continuity of the tissues in the outer and inner cavities or blood spaces of the spiracular gill.

appears to be cell-free. A careful search, both of sections and dissections, failed to reveal a single blood cell.

In the pharate adult stage the cells of the epithelia of both the walls of the gill and the median lamellae apparently form a syncytium, and I have been unable to distinguish cell walls either by staining or by phase contrast microscopy. Mitotic figures were never seen in the epithelia in the pharate adult

stage. In most specimens examined, the nuclei of all four epithelia were 8–10 μ broad, but in one specimen (figs. 7–9) most nuclei were 3–5 μ broad.

The number of cells isolated in the gill is surprisingly large. The area of the gill was obtained by cutting out its outline, drawn with the aid of a camera lucida, on a piece of paper of known area and weight, and then converting loss of weight into loss of area. By this method, the area of one surface of a gill 1.9 $\times$ 0.85 mm. was found to be 1,200,000 μ^2 . This is a minimum figure since it takes no account of the curvature of the gill. In an area of 110,000 μ^2 27 nuclei were counted. This is equivalent to a rate of 294 nuclei per 1.2 mm.². There are four epithelial layers, so that, assuming the density of nuclei in each layer to be 27 per 110,000 μ^2 , no less than 1,176 nuclei or cells are isolated in the pupal gill at the time of the pupa-adult moult. This figure assumes the gill to be flat. It does not allow for the additional cells that result from its curvature, nor does it allow for the loss of epithelial area at the junction of the median lamellae with the wall of the gill.

(a) *Fate of the Cells Isolated in the Spiracular Gill.*

The nuclei of the cells isolated in the gill at the pupa-adult moult show no signs of degeneration throughout the pharate adult phase, which at room temperature is usually about a week. Furthermore, shed pupal cuticles collected in the field sometimes contained nuclei that showed no signs of degeneration. Unfortunately, for lack of the necessary observations at the appropriate time, the maximum duration of the nuclei in the gill before degeneration sets in cannot be determined. However, one pupal exuvium is available which was preserved approximately 24 hours after the adult emerged. The nuclei in the gills of this exuvium show no signs of degeneration (fig. 14) and are equal in size to those of the gill in the pupal stage before the larval cuticle has been shed (fig. 5).

(b) *Possible Selective Value of the Cells Isolated in the Spiracular Gill.*

As already implied, the spiracular gill of the pupa does not function in the pupal stage: it first becomes functional when the larval cuticle is shed, that is, when the insect is a pharate adult. Throughout the pharate adult stage the pupal gill is the principal respiratory organ of the adult (the respiratory significance of the cuticle of the general body surface has not been determined). During the pharate adult stage, which is the only stage in which the pupal gill functions, the gill is only mechanically connected to the living insect. The isolation of about 1100 cells in the pupal gill represents a considerable loss to the insect. This loss may be unavoidable owing to the mechanical difficulties of retracting the epithelium from so complex a structure. Although the simple explanation of the shed epithelium may be that at some stage during the evolution of the gill a degree of complexity was reached which necessitated the shedding of the epithelium, such an explanation does not suffice to account for the formation of the basal occluding membrane of the gill at the pupa-adult moult. It therefore seems possible that the function of the isolated cells during the pharate adult stage may be to repair the pupal gill if it is damaged. In the early summer of next year, when pharate adults again become available, it is intended to carry out experiments to test the possibility that the isolated cells are capable of healing wounds in the spiracular gill.

4. SUMMARY.

1. The structure of the spiracular gill of the Tipulid genus *Lipsothrix* is described and illustrated.

2. The pupal gill of *Lipsothrix* appears to function only in the pharate adult stage, like the respiratory horn of the pupa of another Tipulid, *Crunobia litoralis* Meig.

3. It is shown that in some Tipulids the pupal stage takes place entirely within the larval cuticle, and that by the time the larval cuticle is shed the insect is already in the adult stage.

4. The presence is noted of structures, here called tracheal anchors, which attach the main tracheal trunk entering the respiratory horn or spiracular gill to the body-wall cuticle.

5. It is shown that at the pupa-adult moult about 1100 epidermal cells are isolated from the living animal in the cavities of each prothoracic gill of *Lipsothrix*. These cells do not begin to degenerate until some time after the adult has emerged from the pupa. It is suggested that they may perhaps function in healing wounds to the gill in the pharate adult phase when the pupal cuticle is only mechanically connected to the living animal.

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SIMPLE METHODS FOR REARING THE CRICKET (*GRYLLULUS DOMESTICUS* L.) WITH SOME OBSERVATIONS ON SPEED OF DEVELOPMENT AT DIFFERENT TEMPERATURES.

By J. R. BUSVINE, D.Sc., F.R.E.S.

(*London School of Hygiene and Tropical Medicine.*)

1. INTRODUCTION.

THERE seem to have been remarkably few laboratory studies of the bionomics of that common and well-known insect, the domestic cricket. Cappe de Baillon (1920) gives a few data on its rate of growth and development, in a long paper on the comparative anatomy and physiology of oviposition of crickets and grasshoppers. Herter (1923) investigated the temperature preferences of crickets and Lutz (1932) included them in his studies of rhythms of activity. Bolduirev (1946) records some observations on the influence of different temperatures on crickets which were breeding in and around greenhouses near Moscow.

The largest contribution to the study of the biology of *Gryllulus domesticus* was made by Kemper (1937) who describes the habits, locomotion, feeding, oviposition, development of the insect and its reactions to unfavourable conditions. Kemper's work was fairly precise and quantitative, but suffers from the defect that he did not manage to follow the complete development, since his entire stock died out after two to three months.

The papers quoted either do not describe the methods of rearing crickets in the laboratory or give only a bare outline; also there are few reliable data on the rate of incubation and development. Therefore, it seems worth putting on record the methods used to maintain a colony during the past five years and some observations on development at different temperatures.

This colony was started with a few dozen specimens taken from a municipal refuse dump near Maidenhead. The insects were collected on a mild day in January and it was noted at the time that various sized nymphs were present as well as adults, which were stridulating.

2. REARING METHODS.

(a) *Containers*.—Crickets may be kept in open containers, provided that the walls are of clean glass and more than a few inches high. (Kemper records 6-8 cm. as the maximum height to which they can jump.) Large glass battery jars or small aquaria about a foot square are suitable for the adults, and large glass jars for the nymphs. The bottom of the container is covered with dry sand, to provide foothold. Pieces of folded cardboard may be added to provide harbourages.

(b) *Food*.—The staple diet consists of a meal made up for feeding laboratory animals. It is based on cereals, with proteins and vitamin-containing substances added. The formula given by the manufacturers is as follows: yellow maize meal 35 per cent., wheat feed 20 per cent., "Vitamix" (a by-product of "Bemax" manufacture) 15 per cent., dried milk products 10 per cent., animal

protein 5 per cent., grass meal 5 per cent., arachis oil 5 per cent., dried yeast 3 per cent., linseed cake meal 2 per cent., salt $\frac{1}{2}$ per cent. Shallow trays full of meal are placed in the cricket containers and replenished when necessary.

Occasionally (about once a week) fresh greenstuff, such as cabbage, lettuce or spring greens, is added to the containers. The insects readily feed on these leaves when they are fresh; however, no experiments have been done to determine whether this addition is essential.

(c) *Water*.—Kemper has pointed out that crickets are very prone to cannibalism when short of water. A constantly available water supply is provided by means of a cotton-wool pad in a petri dish, maintained in a damp condition by an inverted tube full of water standing on the surface.

(d) *Collection of eggs*.—The crickets will lay eggs in the damp cotton pads provided for drinking and if these are removed at intervals, eggs of known age can be obtained. For normal breeding purposes, the entire pad can be kept intact, in a jam jar, and kept moist by occasional watering until the young crickets hatch. When standard numbers of eggs are required, as in incubation experiments, they can be picked out of the cotton wool pad, with gentle teasing under a low power binocular microscope.

Browning (1952) who worked with the Australian cricket *G. commodus*, advocates the provision of damp sand, from which the eggs can be extracted by sieving. However, I have found that to maintain the correct degree of moisture in sand is more difficult than with a cotton-wool pad.

(e) *Incubation of eggs*.—The eggs develop best if they are in contact with a thin film of water. On the other hand, if they are placed on wet filter paper in a closed petri dish, they absorb too much water and many swell up and burst.

Satisfactory conditions may be achieved by keeping them on small blocks of plaster of Paris, standing in water. The escape of the young nymphs on hatching may be prevented by confining the eggs in glass cylinders about two inches high. Instead of plaster blocks, strips of filter paper, with one end immersed in water, can be used. However, this is less satisfactory because the strip varies in moisture according to the distance from the wet end.

Whatever method is employed, the cricket eggs are often covered with moulds during the incubation period. I have not been able to find a fungicide which will check mould growth without harming the eggs. However, the fungi are saprophytic and apparently harmless to the eggs.

3. SPEED OF DEVELOPMENT.

(a) *Previous observations*.—Cappe de Baillon is rather vague about the incubation period, which, he states, is variable and dependent on external conditions such as temperature. He does, however, give a series of data for the different stages of nymphal development in an incubator at 28° to 35° C. (see Table I).

TABLE I.—Results of Cappe de Baillon on the rate of growth of the cricket.

Nymphal stage	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Days' duration	3	3	3	4	4	4	5	5	6	7	8
Length of body (mm.)	3	4	5	6.5	8	10.2	12	13.4	15	17	20
Length of ovipositor (mm.).	—	—	—	—	—	—	0.5	1	2	4.5	12.5

The ovipositor appears in a rudimentary form in the fifth stage and the elytra in the tenth stage. He observes that development is much slower at room temperature (a month for the first stage, for example), and that there is more mortality. Cappe de Baillon observes that his crickets always passed through eleven stages, which is a rather high number for the Orthoptera (Chopard, 1938, p. 256). It may be remarked that Yersin had recorded this number for the field cricket (*Gryllus campestris*) as long ago as 1858.

Kemper gives the incubation period of *Gryllulus domesticus* as 8 to 12 weeks at room temperature. The young crickets he hatched from eggs died out after 11 weeks in the fourth and fifth stages. He obtained others about the same size and reared them to adults. By adding the two periods together he estimates 30 to 33 weeks for total development.

(b) *Present observations.*—From time to time batches of about two dozen eggs of known age were incubated at constant temperature and the dates of hatching of the first nymphs recorded. Colonies of crickets were also reared at various constant temperatures and the appearance of the first adults noted.

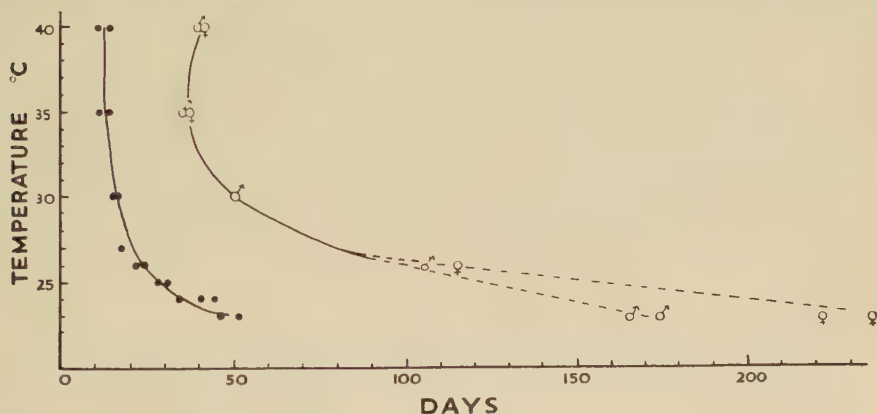


FIG. 1.—Development of the domestic cricket at different temperatures. *Left*: Incubation of the eggs. *Right*: Nymphal development, for males and females.

TABLE II.—*Minimum periods of incubation and development of the domestic cricket Gryllulus domesticus.*

(The several figures under some of the headings are results from different batches.)

Temperature		Days' incubation.	Days development to adult.	
° F.	° C.		Male.	Female.
104	40	11, 14	40	41
95	35	11, 13	35	35
86	30	15, 16	50	?
80.6	27	17	—	—
88.8	26	22, 23	108	115
77	25	28, 30	—	—
75.2	24	34, 40, 44	—	—
73.4	23	46, 51	165, 174	222, 238

The results obtained with various batches are given in Table II and illustrated by fig. 1. It must be admitted that a more precise value would be the *average* rather than the *minimum* times of incubation and development. However, this would have involved more time and attention than could be spared from other work, so the available results are presented for what they are worth.

It may be noted that these results are consistent with the few existing data. Cappe de Baillon's total of 52 days for development corresponds to about 30° C., while Kemper's 8 to 12 weeks' incubation and 30 to 33 weeks' development correspond to a temperature somewhat below 23° C., which would be expected for "room temperature".

4. CONCLUSIONS.

In the laboratory, the domestic cricket can be satisfactorily reared at temperatures between 25° and 35° C. It can complete development at 40° C., but a slight prolongation of the life cycle suggests that this temperature is somewhat unfavourable. At temperatures below 25° C., development is very prolonged, e.g., at 23° C., nine or ten months elapse between oviposition and the emergence of the first females. There does not appear to be a diapause in the egg stage, so that it is not necessary to subject eggs to prolonged chilling to induce hatching, as with *G. commodus* (Browning, 1952).

These facts are consistent with the general opinion that *Gryllulus domesticus* originated in a warm climate and is not adapted for hibernation. In northern Europe, crickets traditionally spend the winter in kitchens and bakeries; but nowadays, more commonly in the warmth of fermenting refuse dumps.

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QUEEN PRODUCTION IN COLONIES OF BUMBLEBEES.

By J. B. FREE.

(*Bee Research Department, Rothamsted Experimental Station, Harpenden.*)

INTRODUCTION.

It has been supposed that the production of queens in bumblebee colonies is brought about by a reduction in the larva/worker ratio, with the result that an increased amount of food becomes available per larva. Frison (1927) expressed this idea as follows: "with fewer eggs or larvae to care for they get better attention and result in the formation of queens." Experimental evidence in support of this hypothesis has so far been lacking.

METHOD AND RESULTS.

In the early spring of 1953, ten colonies of *B. pratorum* were started in the laboratory by confining queens individually in nest-boxes with varying numbers of workers (Table I). An abundant supply of honey and pollen was available in each of the nest-boxes. Eggs were laid within a few days.

TABLE I.—*Bees which emerged from B. pratorum colonies started in confinement.*

Colony No.	Number of workers confined with queen.	Emerged from first brood batch.			Duration of pre-imago stages (days).
		Workers.	Queens.	Drones.	
1	0	+	—	—	27-30
2	0	—	—	—	
3	1	+	—	—	35-36
4	1	—	—	—	
5	1	+	—	—	44-49
6	1	—	—	—	
7	2	+	+	—	21-34
8	5	+	+	—	22-28
9	10	—	—	+	21-27
10	10	—	—	+	22-28

+ = present. — = absent.

No adult bees emerged in colonies 2, 4 and 6, but worker bees emerged from the first batch of brood in colonies 1, 3 and 5. Their weights are shown in Table II. Only drones were produced in colonies 9 and 10; probably some of the numerous workers which were present in these colonies had developed ovaries and laid eggs. Both worker and queen bees emerged from the first batches of brood of colonies 7 and 8.

There did not appear to be any correlation between the weight of a bee and the order in which it emerged (Table III), although the larger bees tended to emerge from cocoons in the centre of the brood batch.

TABLE II.—*Weight (mg.) of female bees which emerged in B. pratorum colonies.*

Colony No. .	Naturally occurring colonies.			Experimental colonies.				
	13.	15.	27.	1.	3.	5.	7.	8.
Weight (mg.)								
20-39	.	.	.	.	.	.	.	.
40-59	1	.	2	1	.	1	.	.
60-79	3	3	4	2	2	2	.	.
80-99	17	18	22	5	1	1	.	1
100-119	19	27	44	1	.	.	.	1
120-139	7	12	28	.	.	.	.	.
140-159	.	3	6	.	.	.	1	.
160-179	.	1	1	.	.	.	.	1
180-199	.	2	.	.	.	.	.	.
200-219	.	2	.	.	.	.	.	.
220-239	.	2	.	.	.	.	.	.
240-259	.	6	3	.	.	.	.	.
260-279	.	5	3	.	.	.	1	.
280-299	.	4	8	.	*	.	1	.
300-319	.	5*	5	.	.	*	1	.
320-339	.	3	3	*	.	.	.	4
340-359	*	4	1	.	.	.	.	2
360-379	.	.	1	.	.	.	*	.
380-399	.	.	1*	.	.	.	.	.
400-419	.	1	3	.	.	.	.	.
420-439	.	.	1	.	.	.	.	.
440-459	.	.	3	.	.	.	.	.
460-479	.	.	5	.	.	.	.	.
480-499	.	.	.	.	.	.	.	.

* = Weight of original queen.

TABLE III.—*Weight of female bees which emerged from the first batches of brood in colonies of B. pratorum started in confinement, showing the order of emergence.*

Order of emergence.	Colony 1.	Colony 3.	Colony 5.	Colony 7.	Colony 8.
1	80	75	95	142	330
2	62	74	77	314	326
3	104	88	65	293	328
4	86	.	52	268	323
5	73	.	.	.	348
6	55	.	.	.	345
7	82	.	.	.	107
8	110	.	.	.	99
9	96	.	.	.	177

No structural or colour differences are apparent between workers and queens of *B. pratorum*, but they may be distinguished from one another by their relative sizes. Furthermore, young queens show a tendency to develop large fat-bodies, which workers do not, and development of their ovaries also tends to be delayed until the following spring (Cumber 1949, Free 1955).

In Table II the weights of bees in three naturally occurring *B. pratorum*

colonies are shown. Colony 13 was in a relatively early stage of development, whilst colonies 15 and 27 were producing queens. It would appear from the frequency distribution of bees of different weights in these colonies that bees weighing more than 240 mg. can safely be assumed to be queens. Three of the bees which emerged in colony 7 and six in colony 8 were above this weight. When these large females were a week old they were put into a glass arena with 70 to 80 drones, and copulation was frequently seen to occur. This alone strongly suggested that these bees were queens, although the evidence could not in itself be considered conclusive, since attempted matings between workers and drones have sometimes been observed.

A month after emergence these supposed queens were dissected and found to contain the large fat-bodies typical of "autumn" queens. Their ovaries had remained undeveloped, although in colony 8, which had become queenless, the ovaries of some of the workers present had developed.

These facts, together, show conclusively that queens were produced from the first batches of eggs laid by the queens of colonies 7 and 8.

More queens, of a greater mean weight, emerged from colony 8, where five workers helped the queen, than from colony 7, where only two were present.

DISCUSSION AND CONCLUSIONS.

Frison (1927) observed that "the first workers produced were comparatively small, and that the workers averaged larger and larger as the season progressed." He thought that the increase in size of workers was correlated with their nutritional conditions. Richards (1946) classified the workers from *B. agrorum* colonies into three age-groups—according to the condition of their coats. He found that "the fresher workers are larger, suggesting a progressive change in the development of the colony."

Cumber (1949) analysed the weights and wing lengths of bees which he found in *B. agrorum* colonies at different stages of development. He concluded that there was no gradual increase in the mean size of workers, although there might have been a tendency for some of them to become larger as the season progressed, and that there was a sudden increase in the mean size of female bees at the time of queen production. Data were obtained by the author from *B. agrorum* colonies by a similar method to that used by Cumber and similar results were obtained. However, this method of estimating the seasonal variation in worker size is subject to two possible errors:

(a) It allows for no consideration of the relative longevity of house-bees and foragers. Brian (1952) showed that house-bees generally live longer than foragers, and since the latter are the larger bees (Richards 1946, Cumber 1949, and Brian 1952) the size of the workers which have been produced in a colony will be greater than that of those bees which are present when it is collected. The relatively greater proportion of small to large bees which is present in nests later in the season (Cumber) is likely effectively to offset any weight increase resulting from the production of larger bees, and the average weight will tend to remain constant.

(b) It is rarely possible to capture all the bees when a colony is collected, and a high proportion of those which escape are foragers. Their numbers will of course, be greater in the case of a large colony with its larger numbers of foragers.

When these two factors are taken into account, Cumber's results are more in agreement with those obtained by Frison and Richards, although they do not invalidate Cumber's conclusion that a sudden increase in the mean size of female bees takes place at a certain stage of the development of the colony—these larger bees being queens.

Sladen (1912) considered that "an abundant supply of food is not sufficient to make a female larva develop into a queen, but that it may be necessary for the larva to be from an egg that has been laid late in the queen's life." Later, however, he performed an experiment in which he combined two colonies of *B. latreillellus* in such a manner that there were 20 workers to care for three eggs. Each of these eggs developed into "females as large as queens."

Until the present work this single uncontrolled experiment was the only direct experimental evidence that queen production in *Bombus* is dependent on the existence of a low larva/worker ratio.

Cumber (1949) described a *B. lucorum* colony in which queens were produced much earlier than usual, following the death of the original queen. He suggested that as a result of a change in the larva/worker ratio the larvae, which had hatched from eggs laid late in the queen's life, had received sufficient food to cause them to develop into queens. Similar evidence was provided by the author, who found that the last two eggs laid by the queen of a *B. sylvarum* colony, before she disappeared, developed into queens.

Results obtained from colonies kept in confinement in nest-boxes, clearly demonstrate that queen production depends not only on the presence of an abundant food supply, but also on a certain minimum amount of attention being given to the developing larvae, as in colonies 7 and 8, where two and five workers respectively were present to help the queens. It seems highly probable that, under natural conditions, queens are only produced when both these conditions are satisfied.

Gerstung (1891–1926) pointed out that when a queen honeybee reaches her maximum output of eggs there must be an decrease in the brood/worker ratio, and he concluded that this results in more food being available per head of brood, and hence to the lavish feeding of some larvae to produce queens. Although in the light of recent work (Demuth 1922, Hess 1942, Butler 1954 and Simpson 1954) this hypothesis has had to be rejected in the case of honeybees, it would seem to account for the known facts of queen production in bumblebee colonies.

By analogy with the results from other population studies, it is likely that the egg laying cycle of queen bumblebees assumes the form of a sigmoid curve. A curve of this form would account for the sharp difference which Cumber observed in the larva/worker ratio between bumblebee colonies which were and which were not producing queens. He found that the larva/worker ratio of *B. agrorum* colonies "must approach or fall below 1 before queen brood is produced," and he produced evidence which suggests that the rate of egg laying by a queen bumblebee may fall off slightly towards the end of her life.

Cumber found that in the pocket-making species there tended to be a continuous range of size from workers to queens, but in the pollen-storing species there was a definite distinction between the body sizes of workers and queens. His results have been confirmed (Free unpublished) although it has been found that the size difference between workers and queens of *B. pratorum*

colonies (pocket-making species) is probably not as great as that in some of the other pollen-storing species.

Buttel-Reepen (1903), Sladen (1912), and Cumber (1949) suggested that the competition for food amongst larvae of the pocket-making species accounts for the continuous curve of body size of females found in colonies of these species. This is probably also to some extent true of colonies of *B. pratorum*, where the larvae likewise remain together in a single group. The larvae of some of the pollen-storing species become separated from each other early in their development, and each probably receives more uniform attention, so that when there is an abundance of food in the nest it is probable that they nearly all develop into queens, and no females of intermediate sizes occur as they do in colonies of the pocket-making species.

Cumber concluded that the larva/worker ratio in colonies of *B. agrorum* (pocket-making species) may be controlled to some extent by workers eating some of the eggs which are laid by the queen and that increased egg destruction by the workers results in the production of sexual forms. As Brian (1951) pointed out, however, "a steady rate of egg destruction, in conjunction with the queen's normal egg laying cycle would be sufficient to produce the desired result." Brian did not notice any egg eating by the members of two *B. agrorum* colonies which she had under observation, and suggested that the disappearance of eggs which occurred may have been due to cannibalism by the young larvae.

Egg-eating by workers of pocket-making species has only been observed in colonies of *B. fervidus* (Plath, 1934). It has not been observed in the several large colonies of *B. agrorum* kept by the author. It occurred in the case of a *B. sylvarum* colony only when it was kept in confinement, and the workers were fed solely on a carbohydrate diet. The habit of egg-eating has, however, been frequently observed in *B. lapidarius* and *B. terrestris* colonies (pollen-storing species) at the time of queen production (Huber 1802, Jardine 1840, Hoffer 1882-3, Grimshaw 1887, Haviland 1887, Härter 1890, Sladen 1912, and Lindhard 1912). It has also been seen by the author to take place in a colony of *B. lucorum*, but not in several *B. pratorum* colonies which were under observation.

It is therefore possible that egg-eating by the workers of certain pollen storing species may be a contributory factor to the sudden lowering of the larva/worker ratio and the elimination of females intermediate in size between workers and queens.

Since queens were derived from the first batches of eggs laid by the queens in colonies 7 and 9—eggs which would normally only produce small workers (as in colonies 1, 3 and 5), and since both queens and workers emerged from the same group of cocoons in colonies 7 and 8, it appears that there is no inherent difference between the eggs from which queens and workers are produced.

Since the workers in colonies 7 and 8 all emerged from the outside cocoons of the brood clumps, their small size was probably due to lack of success in the competition for food (see above) rather than to any qualitative difference in the food supplies. Free (1955) concluded that the pharyngeal glands of worker and queen bumblebees do not produce special brood food equivalent to that which is produced by the pharyngeal glands of worker honeybees (Schiemann 1883, Langer 1912), so that any difference in the type of food

supplied to worker or queen-producing larvae is less likely to be found amongst bumblebees than amongst honeybees.

Sladen (1912) and Frison (1927) found that the pre-imaginal stages of queens lasted longer than those of workers. Since this was not true in the experiments mentioned above it would seem that the duration of the developmental stages does not by itself play an important part in the production of queen bumblebees. Queen honeybees take less time to develop than do worker honeybees (Huber 1792 and 1814).

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SUMMARY.

1. Queen bumblebees have been induced to found colonies by confining them with varying numbers of workers and an abundance of food.
2. When a sufficient number of workers were present to help the queen some of the first eggs laid by her developed into queens.
3. The factors which lead to the production of queens in naturally occurring bumblebee colonies are discussed.

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COMMUNICATION BETWEEN HONEYBEES: II. THE RECRUITMENT OF TRAINED BEES, AND THEIR RESPONSE TO IMPROVEMENT OF THE CROP.

By C. R. RIBBANDS, M.A., F.R.E.S.

(*Bee Department, Rothamsted Experimental Station, Herts.*)

INTRODUCTION.

INVESTIGATIONS into the circumstances in which successful foragers dance on their return to the hive have hitherto involved observations of the dances themselves (von Frisch, 1923, 1934, 1942; Lindauer, 1949).

The present results were obtained by a method which needed less labour and less skill. The dances were not observed, but their extent could be inferred from counts of the number of recruits attracted to feeding places. The effect of change in the concentration of the sugar syrup supplied at these feeding places was investigated.

METHOD.

Two kinds of sugar syrup were used in these experiments; concentrated syrup contained 2 lb. sugar dissolved in 1 lb. water, dilute syrup was made by diluting one volume of concentrated syrup with three volumes of water.

A colony of yellow bees was set down in a district in which the rest of the honeybee population were dark in colour. The vicinity of the hive was plentifully supplied with recognition marks (a house, a barn, high walls, a copse, trees, hedges and paths).

Three Petri dishes, *a*, *b*, and *c*, were placed at a distance from the hive of (a) 50 yards; (b) 60 yards, and at an angle of 73° to *a*; (c) 72 yards, and at an angle of 126° to *b*, and 199° to *a*. On 16th August, 1951, three groups, A, B and C, each of 36 bees from the colony, were trained to collect concentrated syrup from dishes *a*, *b*, and *c* respectively, and the bees were individually marked. All other bees which came to the dishes were killed. On the following day dilute syrup was supplied to all three dishes and training was continued.

The experiments were carried out on 18th and 20th August, 1951. The syrup concentrations in the dishes were varied, and the effect of the variations was measured by observers, who killed all recruits to the dishes, and studied the behaviour of the marked guide bees.

RECRUITMENT OF THE TRAINED BEES.

In each experiment, the time of the first visit of each trained bee was noted. The number of arrivals at successive 5-minute intervals is given in Table I. The feature of these results is that there was independent recruitment to the three dishes, which were at similar distances but in different directions, and supplied with unscented syrup which differed from dish to dish only in its water

content. Moreover, the independence demonstrated that recruitment of the trained bees really did occur, and that their sudden appearance was not due to some change in weather conditions.

The independence of the recruitment indicates that the trained bees had followed the dances of their similarly-trained comrades, and responded to the indication of direction which they gave. This result complements the observation of von Frisch (1950), who found that two groups of bees, trained to scentless dishes of syrup either close to or far from the hive, responded only to the dances of bees which had been foraging at the appropriate distance.

In favourable conditions recruitment is very rapid. For instance, on the afternoon of 20th August dish *b* was put down at 13.20 hrs. G.M.T. and the first trained bee arrived at 13.36 hrs. Two others came at 13.38, and another one at 13.39—the absence of bees at dish *c* indicates the probability that these bees were recruited by the first bee on its first return to the hive; it returned itself at 13.39. Another bee arrived at 13.41, two at 13.42, two at 13.43, four at 13.44, one at 13.45, one at 13.46, one at 13.48, one at 13.49, two at 13.51, one at 13.52, one at 13.54. One other did not come until 15.15 (perhaps alerted by vigorous dancing after the increase in syrup concentration at 15.00 hrs.).

It is surprising that 15 out of 22 trained bees came within 10 minutes of the first arrival, and 21 out of 22 within 18 minutes. This rate of recruitment of marked bees exceeds that observed by von Frisch (1920), who found that 18 out of 24 trained bees arrived at a dish within half an hour of the arrival of the first one.

RECRUITMENT OF TRAINED BEES TO OTHER POSITIONS.

There were two instances of marked bees which went to a dish other than that to which they had been trained. Both occurred on the afternoon of 20th August and involved desertion from dish *b*. One of the marked bees, which paid four visits to the dilute syrup in that dish between 13.48–14.25 hrs., was subsequently killed when it visited the concentrated syrup at dish *a* at 14.55 hrs.; the other bee was killed when it visited the dilute syrup at dish *c* at 14.30 hrs., having paid seven visits to dilute syrup at dish *b* between 13.49 and 14.20 hrs.

SCENTING BY THE TRAINED BEES.

Five of the 22 trained bees were seen to expose their scent gland on arrival at the dilute syrup in dish *a* on the morning of 20th August; each did so on at least two occasions, and one did so on at least five occasions.

At 11.00 hrs. the dilute syrup at this dish was replaced by concentrated syrup, and after each bee had made a few visits, scenting became usual instead of exceptional; 13 of the 22 bees then scented at every visit and others did so on some visits, but even in these circumstances two bees came regularly, but they did not expose their scent gland at all while they were on the dish (one bee was scenting when visiting the dilute syrup at dish *b* at this time).

Thus the strength of stimuli required in order to produce scenting differed considerably among individuals from the same colony foraging in identical conditions.

On the afternoon of 20th August the presence or absence of scenting was

carefully recorded at each visit to dish *a*, which was continuously supplied with concentrated syrup, and to dish *b*, which was supplied with dilute syrup until 14.40 hrs. and then with concentrated syrup; when scenting commenced, this happened not earlier than the second, or later than the sixth, visit to the concentrated syrup (3.2 trips, the mean time of commencement at dish *b*, where the concentration was raised, was insignificantly shorter than the mean of 3.7 trips at dish *a*, where concentrated syrup was continuously supplied).

NUMBERS OF TRAINED BEES ON THE DISHES.

The numbers of marked bees coming to the dishes *a*, *b* and *c* are recorded in Table I. As it was not found possible to record each visit of each individual bee, on 20th August the number of bees on each dish was recorded at 5-minute intervals. Changes in the syrup concentration did not significantly affect the rate of visiting. The data indicated that changes in the rate of visiting at the dishes were insufficient to affect materially the results which follow in the next section.

TABLE I.—*Number of trained bees recruited to the dishes in successive 5-minute intervals.*

18th August, from 08.40 hrs. G.M.T.

Dish.	Syrup.	0-5	-10	-15	-20	-25	-30	-35	-40	-45	-50	-55	-60
<i>a</i> ,	+	.	.	3	7	7	5	3	1	1	.	1	2
<i>b</i> ,	++++	9	8	9	1	4	.	.	.	.	.	.	.
<i>c</i> ,	+	.	.	12	9	4	4	.	1	.	.	.	.

20th August, from 08.55 hrs. G.M.T.

Dish.	Syrup.	0-5	-10	-15	-20	-25	-30	-35	-40	-45	-50	-55	-60
<i>a</i> ,	+	9	4	3	1	.	.	1	.	.	.	1	.
<i>b</i> ,	+	.	7	12	2	.	1	.	.	.	.	.	.
<i>c</i> ,	++++	10	11	4	1	.	.	.	.	.	2	.	.

20th August, from 13.20 hrs. G.M.T.

Dish.	Syrup.	0-5	-10	-15	-20	-25	-30	-35	-40	-45	-50	-55	-60
<i>a</i> ,	++++	1	.	.	6	2	.	5	1	.	1	.	.
<i>b</i> ,	+	.	.	.	4	9	4	4	.	.	.	.	1
<i>c</i> ,	+	.	.	.	.	.	2	10	5	3	2	.	3

EFFECT OF SYRUP CONCENTRATION ON NUMBERS OF NEWCOMERS.

In each experiment one dish contained dilute syrup and one was filled with concentrated syrup; the third dish at first contained dilute syrup, which was subsequently replaced by concentrated syrup. In the three experiments the different concentrations were supplied in turn at the three sites.

The results are presented in Table II. During the first, or control, period of each experiment many more bees were always attracted to the dish which contained concentrated syrup than to either of the dishes with dilute syrup, but the ratio between the numbers attracted to the two concentrations varied markedly (from 40.5:90 up to 10.5:185). The cause of this variation is

unknown¹; it is unlikely to have been due to differences in the concentration during previous training periods, because at the two dishes supplied with dilute syrup the numbers of recruits attracted were unexpectedly alike.

TABLE II.—*The concentration of sugar syrup in the dishes, and the number of recruits attracted to them.*

	Dish a.		Dish b.		Dish c.	
	Syrup.	Recruits attracted.	Syrup.	Recruits attracted.	Syrup.	Recruits attracted.
18th August						
08.40–10.30 hrs.	+	41	++++	90	+	40
10.30–11.30 hrs.	+	21	++++	60	++++	129
20th August						
09.00–11.00 hrs.	+	11	+	10	++++	185
11.00–12.00 hrs.	++++	63	+	5	++++	33
20th August						
13.40–14.40 hrs.	++++	59	+	7	+	7
14.40–15.45 hrs.	++++	47	++++	128	+	2

During the second period of each experiment, twice as many recruits were attracted to the concentrated syrup in the dish in which the concentration had been recently raised, as to the concentrated syrup in the other dish, in which it had been supplied for some time.

EFFECT OF DISTURBANCE ON NUMBERS OF RECRUITS.

In an experiment which was subsequently carried out, and which has been published elsewhere (Kalmus and Ribbands, 1952, Experiment 12), a group of marked bees were trained to collect concentrated syrup from a dish, and on two occasions the dish was removed and immediately replaced by a similar dish, not previously used, and therefore not impregnated with bee scent. Although the marked guides soon settled down to forage at the new dish, the number of recruits attracted to the vicinity was temporarily reduced after each change.

In two hours prior to the first change, 50 recruits were attracted, and the numbers attracted during 10-minute intervals thereafter were 1, 10, 5, 5, 12, 12. (The reduction in the first period was not due to absence of bee scent on the dish, because the bee-scented dish was placed about a yard away, and recruits attracted to either dish were counted.) The dish was then changed again, and the recruits arrived thus: 1, 3, 4, 7, 8, 5.

These results suggest that the slight disturbance of the foragers caused by the change of dishes may have been sufficient to reduce their dance activity.

¹ On the morning on which the ratio of recruits attracted to the dilute syrup was highest during the preliminary period it was also highest during the subsequent experimental period (21 : 129; next highest ratio for a similar pair of dishes 5 : 63). This suggests that the differences were not entirely fortuitous; perhaps conditions elsewhere on this morning were less satisfactory, so that bees were more easily incited to dance by dilute syrups.

DISCUSSION.

(a) *The relation between dancing, scenting and recruiting.*

Von Frisch (1923) observed that foragers which had danced often returned to their feeding-place with their scent organ exposed. Dancing and scenting are probably both induced by the same stimuli, but the correlation between dancing and scenting is not complete—a bee may dance without subsequently scenting, or *vice versa* (Ribbands, 1953).

Dancing produces recruiting, and scenting facilitates it. Thus, a high correlation between these processes is to be expected. Lindauer's (1949) demonstration that the threshold concentration of sugar syrup required to induce dancing varied seasonally, and was related to weather and alternative food supplies, shows that the dances are most frequently performed when they are most likely to meet with a response; this increases the correlation.

These considerations suggest that for many purposes it is legitimate to examine recruiting and scenting phenomena, which are easily observed, and to infer that they bear a close relation to dancing, which is less easily and less quickly studied.

(b) *The circumstances in which recruiting occurs.*

Dancing has been shown to increase with the abundance (von Frisch, 1923) and the concentration (von Frisch, 1934) of the syrup supply available. It is reduced by increases in its viscosity or salt content (von Frisch, 1942). Von Frisch concluded that taste was the main incitement to dance activity, but that a psychological factor seemed to be involved, because the same sugar concentration might produce active dances when there was no nectar flow, but be ineffective when a good crop was available elsewhere.

Lindauer (1949) found that the threshold concentration of sugar syrup required to induce the dances varied seasonally, and sometimes from day to day; it ranged from 2 M during the June nectar flow to $\frac{1}{3}$ M in late July. He found that the proportion of dancing bees could be slightly increased by the addition of attractive flower odours to the syrup, or reduced by the addition of skatol. In the results now presented, twice as many recruits went to concentrated syrup in the dish in which the concentration had been recently raised, as to similar syrup in the dish in which it had been supplied for some time. This result is complementary to the observation that a deterioration in the quality of a food supply temporarily inhibited dancing by individuals, which subsequently danced in response to the deteriorated supply (Lindauer, 1949), and to the reduction in recruitment after disturbance of the guides, mentioned earlier.

All these results show that there is no absolute threshold of stimulus which will excite foragers to dance. They seem to respond to a wide variety of factors, and dance the more readily according to the extent to which their crop exceeds in quality any supplies of which they have recently been aware, either by direct experience, or through receiving food from their companions. The stimulus must be something which suits the needs of the community at that time; Park (1923) reported that water collectors danced in springtime, and Lindauer (1949) found that bees which collected pollen substitutes would only

dance if their colony lacked pollen; one may suppose that propolis-collectors will also dance in appropriate circumstances.

Lindauer reported that bees did not dance until they had paid several visits to a food source (at or near threshold syrup concentrations). The arrival times of the recruited trained bees at dish *b* on the afternoon of 20th August are only consistent with the supposition that the first arrival danced on her first return to the hive, and on that afternoon nine previously-trained bees exposed their scent-organs on their second visit to the food source.

(c) *Individual variation in recruiting propensities.*

Lindauer (1949) noticed that different individuals varied in their dancing propensities; one would expect any such differences to be emphasised in the threshold-for-dancing conditions of his experiment.

The present results show that the individual variations in respect of the syrup concentration which induced scenting were surprisingly great. Some bees did not expose their scent organs, even after repeated visits to concentrated syrup, whereas a few of their similarly-trained comrades did so while visiting syrup of only one-fourth of this concentration.

There are other examples of substantial variations in the behaviour of individual honeybees (Ribbands, 1953), so this variation is not exceptional. As all the honeybees of any one colony are sisters, and as honeybee communities have achieved a considerable degree of independence of their environment, some might, perhaps, expect that individual behaviour would be fairly uniform, but further consideration suggests that a wide range of variation in individual behaviour may be of advantage to social insects. For instance, if all the foragers responded to the same range of stimuli in the same manner, their methods of communication might be less effective—sudden favourable conditions might induce many bees to go in search of crops which were not available, whereas it is more economic for a few to act as scouts and to inform their comrades of any success.

In the past there have been many unjustified attempts to draw parallels between social insects and human societies, but there may, nevertheless, be some valid general points of comparison. For instance, good methods of communication between members are the basis of co-operation in any effective society. It is perhaps true of some vertebrate societies that community life enables a greater diversity of individuals to develop, survive, and be useful to the community, because some may possess qualities which enable them to be peculiarly well fitted for a particular occupation, but which would render them unfitted to survive in isolation. If that is so, is it possible that, for a parallel reason, social insects may show a greater diversity in individual behaviour than their non-social relatives?

SUMMARY.

Equal numbers of individually marked bees from one colony were trained to forage from each of three Petri dishes placed in different directions from the colony. Dilute sugar syrup was supplied at one dish, concentrated syrup at another; at the third dish dilute syrup was supplied at first, and then replaced by concentrated syrup. The dish at which the supply improved then attracted

twice as many recruits as did the dish at which concentrated syrup was always available.

Although the three dishes were only 50–72 yards from the hive, the trained bees were separately recruited to them. Previously-trained bees recruited on their first return to the hive, and exposed their scent organ during their second visit to the food source: Individual differences in the behaviour were impressive.

The implications of these results are discussed.

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THE IMMATURE STAGES OF *PENTARTHURUM HUTTONI* WOLL. (COLEOPTERA : CURCULIONIDAE)

By S. M. HAMMAD, B.Sc.Agric.(Cairo), Ph.D.(Bristol), F.R.E.S.

(Faculty of Agriculture, Alexandria University.)

1. INTRODUCTION.

Pentarthrum huttoni is widely distributed in England and Ireland. Both the adults and larvae of this insect have been reported to cause damage to sapwood as well as heartwood. Both hardwoods and softwoods are liable to infestation. Several instances have been recorded (Anonymous, 1940) of the occurrence of this weevil's damage in plywood and panelling of birch, alder and oak. The specimens on which the present work is based were found infesting birch plywood in a damp cellar. The adhesive in the birchwood was blood albumen. The wood was infested with fungi.

The insect was successfully bred in the laboratory at a temperature of 25° C. and a relative humidity of 95–100 per cent.

2. LIFE HISTORY.

(a) *The Egg.*

About four days after mating, the female lays her eggs singly in holes excavated with the mandibles or in already existing cracks and crevices in the wood. The hole is then sealed with a layer of semi-transparent white material exuded from the ovipositor.

Two females laid 50 eggs within 80 days. The eggs were obtained for observation, as recommended by Parkin (1934) for *Lytus*. The transverse surfaces of the wood were first cleaned with a razor blade, in order to open as many pores as possible. The samples were then examined by carefully shaving off thin sections under the binocular microscope.

About 11 days after the egg has been laid the mandibles of the developing larva may be seen through the egg-shell. The head-capsule is at the flat end of the egg and the young larva hatches after 16 days. The egg-shell is ruptured by means of hatching spines or egg-bursters on the sides of the first, second and third abdominal tergites.

(b) *The Larva.*

The shell is completely consumed in about 24 hours, and after this the larva commences to feed on the surrounding wood. The first instar always makes a hole at the surface. Having formed this hole to the exterior, the larva turns inwards at about 45° to the wood surface. After burrowing into the wood for a short distance, the tunnels are made parallel to the surface.

From Dyar's law, the larva has five instars as follows :

1st instar larva :	width of head-capsule	.	0.20-0.24 mm.
2nd "	" " " "	.	0.29-0.33 "
3rd "	" " " "	.	0.39-0.43 "
4th "	" " " "	.	0.50-0.54 "
5th "	" " " "	.	0.59-0.63 "

The larvae pupate in six to eight months after hatching. When the larva is fully grown it constructs a pupal cell, which becomes lined with a soft cushion of fungal hyphae. In this cell the larva becomes sluggish, stretches out, and the head is now completely evaginated from the prothorax. This is the pre-pupal stage of the last instar larva. It lasts two days, and then the last larval cuticle is shed.

(c) *The Pupa.*

The duration of the pupal stage is about 16 days.

(d) *The Adult.*

The cuticle of the adult weevil continues to darken for at least three months. The adult weevil measures about 2.5-4 mm. in length. The antennae are inserted at the middle of the rostrum, the funiculus is 6-segmented and the scape is thickened at the distal end. The tarsus of each leg is 4-segmented.

As in most weevils, the females only differ from the males in having a thinner and longer rostrum. In both sexes, the rostrum is about twice as long as the head. The rostrum of the female is used in making holes in which the eggs are deposited, but, as Imms (1948, p. 528) remarks of weevils in general, the significance of the rostrum in the male is unknown.

The habit of feigning death is well developed in this weevil. It is interesting to note that the males are easy to remove from the surface of the wood, even with a brush, but the females are always difficult to remove, as they attach themselves firmly to the wood by clasping the surface, chiefly with the spines on the distal ends of the tibiae.

The adult weevils make exit holes from their tunnels at an angle of about 45° with the surface of the wood. These holes are irregular in shape and measure about 1.5-2 mm. in diameter. There are, therefore, two sizes of holes on the wood surface, those made by the first instar larvae and those made by the adult weevils.

From the deposition of eggs until the emergence of the adult weevils takes seven to nine months. It has been found possible to breed them on dry cakes of wholemeal flour plus 10-15 per cent. yeast. These cakes were made about as thick as plywood. On this artificial diet the life-history was shortened to about four to four and a half months. The adult weevil lives for about sixteen months after emergence.

It has been stated before that the wood infested by *Pentarthrum* was also infected with fungi, which were found in the wood itself, pellets, frass and dried eggs, dead larvae and adults. The colour of the wood covering the tunnels was paler than that of the outer parts of the wood, while at the same time, fungi were more abundant on the inner surface of the weevil galleries than away from the galleries. The paler colour of the wood covering the galleries may be due

to the difference in structure between this wood and that of the other parts. The fungus is eaten with the wood by the insect, and so, perhaps, supplies it with some of its protein requirements, as well as vitamins (Hendee, 1935).

3. EXTERNAL MORPHOLOGY OF THE IMMATURE STAGES.

(a) *The Egg* (fig. 1A).

Flexible and conforming to the shape of the egg-cavity in the wood. Shining white, unsculptured, very fragile and rather broader at one end than at the other; the broader end resting inward. Rounded towards broader end, but rather flat at other end.

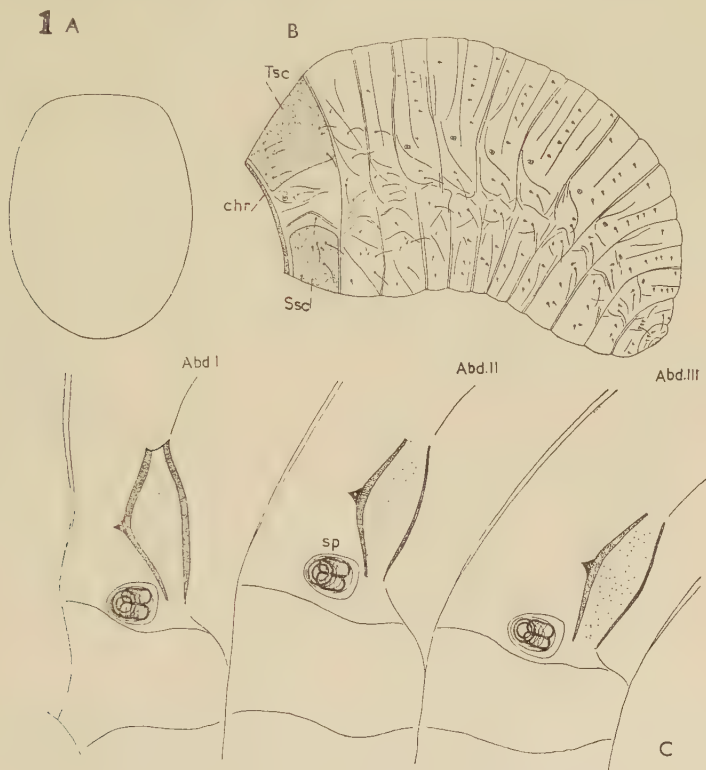


FIG. 1.—A, egg, $\times 80$. B, lateral view of cuticle of mature larva, $\times 167$. C, hatching spines, $\times 1000$. Abd. I—Abd. III, abdominal segments 1–3; chr, chitinous ring; sp, spiracle; Ssc, sternal sclerite; Tsc, tergal sclerite.

(b) *The Larva*.

(1) *Mature larva*.—Body moderately stout and subcircular in cross section, pearly white in colour and strongly convex dorsally, but ventrally much less convex. About 3.3 mm. long and about 0.1 mm. wide (in the widest part, i.e. the middle of the third thoracic segment). Whole cuticle covered with extremely fine, conspicuous sclerotised spines (asperities). Pronotum covered with a sclerite which covers almost the entire tergite. Sternum and pedal lobes of prothorax also covered with a sclerite covering almost the entire sternite. Chitinous ring around the whole anterior margin of prothoracic segment. The

anus is a small transverse cleft at the posterior end of the tenth abdominal segment. Thoracic and abdominal segments with setae as shown in fig. 1B.

Head deeply retracted into thorax. Shape and setae as shown in fig. 2A, B; one pair of ocelli on each side, the dorsal pair being smaller. Antenna (fig. 3C) as figured. Mandibles (fig. 3A, B) of both sides more or less similar; each with an apically produced tooth. Inner edge with large central tooth divided into two large and two small teeth. Molar parts flat and blunt. Dorsal side of each mandible with two long setae; ventral side with only one sensillum. Epipharynx with setae as shown in fig. 3D; provided with two stout long rods

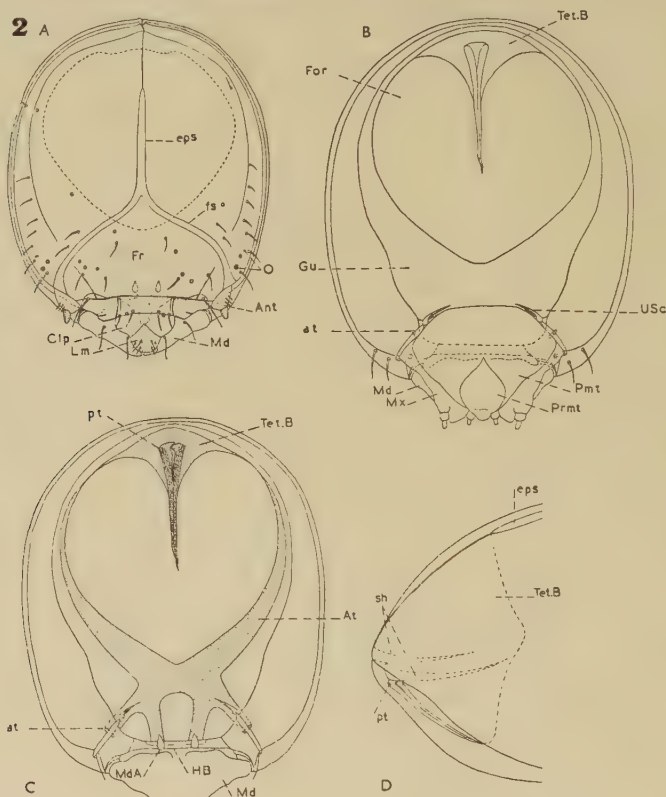


FIG. 2.—Head of larva. A, dorsal view, $\times 70$. B, ventral view, $\times 80$. C, ventral view to show the tentorium $\times 80$. D, lateral view of tentorial bridge, $\times 75$. *Ant*, antenna; *At*, anterior tentorial arm; *at*, anterior tentorial pit; *Clp*, clypeus; *eps*, epicranial suture; *For*, foramen magnum; *Fr*, frons; *fs*, frontal suture; *Gu*, gula; *HB*, hypostomal bridge; *Lm*, labrum; *Md*, mandible; *MdA*, mandibular apodeme; *Mx*, maxilla; *O*, ocelli; *Pmt*, postmentum; *Prmt*, prementum; *pt*, posterior tentorial pit; *sh*, shelf-like processes; *Tet B*, tentorial bridge; *Usc*, U-shaped sclerite.

extending to posterior margin of clypeus. Maxilla and labium with palpi and setae as shown in fig. 3E, F. *Tentorium* (fig. 2C): Formed by two pairs of cuticular invaginations, the anterior and posterior tentorial arms. Posterior tentorial arms arising from posterior tentorial pits and they are continued in a transverse projection, forming a tentorial bridge, through back of head-capsule. This tentorial bridge with two shelf-like processes along each side, as shown in fig. 2D. Each anterior tentorial arm composed of three parts: lateral one arising from anterior tentorial pit; posterior one, attached to the tentorial

bridge near its anterior ends; anterior one attached at its free end to hypostomal bridge. Whole tentorium enveloped by a thin epithelial layer.

(2) *First instar larva*.—Similar in appearance to mature larva. Length of body about 0.5 mm., diameter about 0.24 mm. Head circular in outline and very pale in colour.

(3) *Hatching spines*.—Three pairs of egg-bursters are found in the first instar larva on the sides of first, second and third abdominal tergites (fig. 1c). Similar in shape, each consisting of a simple short, strongly-sclerotised and anteriorly directed spine on a broad sclerotised transverse base. Each base about 0.02 mm. across, lying nearly at middle of tergite, its lower margin being level with the spiracle.



FIG. 3.—A, dorsal view of right mandible, $\times 318$. B, ventral view of mandibles and anterior end of fore-gut in section, $\times 250$. C, antenna, $\times 175$. D, epipharynx, $\times 175$. E, ventral view of maxillae and labium, $\times 156$. F, dorsal view of same, $\times 163$. *Abd.Md.*, mandibular abductor; *c.m.*, circular muscles; *In.*, intima; *Phy.*, pharynx; *sch.*, sclerotised bar.

(c) *The Pupa* (fig. 4):

Uniformly white when first formed. About 3.5 mm. long, 0.1 mm. wide. Tips of wing pads reaching fifth abdominal sternite. Each leg with a long seta on or near knee. Front legs extending almost to proximal margin of first tarsal segment of middle pair. The latter extending almost to apical third of first abdominal sternite. Hind pair extending to posterior margin of third abdominal sternite.

Head completely concealed from above by pronotum. Rather rounded; rostrum elongated and slender. Head with four setae on either side of cranium. Rostrum with

one pair of small setae near its base, two pairs slightly anterior to first pair, and four pairs of very small setae on apex. Antenna extending posteriorly almost to third of front tibia.

Pronotum with six setae on each lateral margin, anterior seta much smaller than other five. Also two setae near middle of pronotum and two others on each postero-lateral angle of pronotum. *Mesonotum* and *metanotum* each with a pair of setae at about basal third on each side.

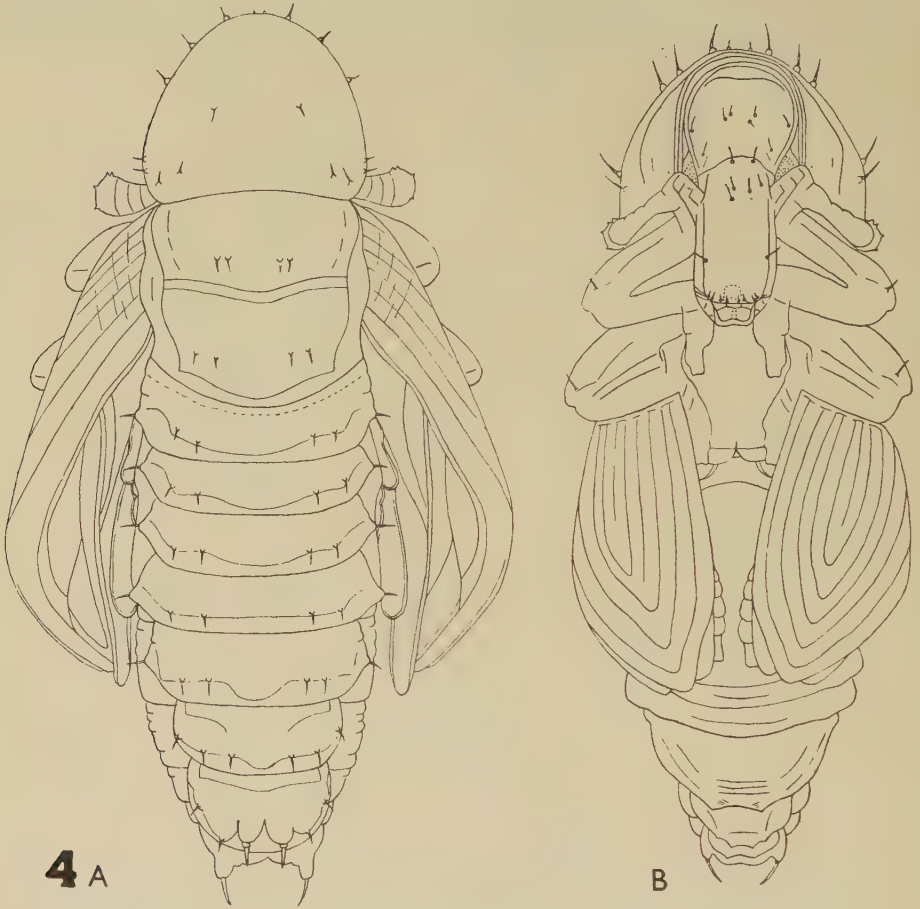


FIG. 4.—Pupa. A, dorsal view. B, ventral view. Both $\times 35$.

Abdomen with seven distinct tergites, becoming progressively larger towards posterior end, the seventh tergite being the largest. Dorsal area of each tergite with one pair of setae on either side, situated about a third of length from posterior border. Lateral area of each tergite provided with one seta mounted on small lobe. Internal pair of setae of seventh abdominal segment much larger and stronger than the others. These two setae mounted on two large lobes and directed forward in the shape of a hook. Last larval skin always remains attached to these two hooks until emergence of adult insect. The ninth abdominal segment with two fleshy processes, each carrying a strong spine directed posteriorly.

4. ACKNOWLEDGMENT

I wish to thank Dr. H. E. Hinton for his keen interest in the progress of the work, and for providing me with a culture of the species.

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NOTES ON A LABORATORY COLONY OF *Aedes (Stegomyia) albopictus* (Skuse) AND ITS DISTRIBUTION IN MAURITIUS.

By JAMES G. HALCROW, B.Sc.(Hons.).

(*Entomologist, Insect-Borne Diseases Division, Mauritius.*)

WITH the destruction in many countries of *Ae. aegypti* L., the vector of yellow fever, the need frequently arises for a suitable test mosquito for bio-assay work. This paper outlines the establishment and maintenance of a colony of *Ae. albopictus* (Skuse) over a period of eighteen months.

DISTRIBUTION IN MAURITIUS.

Ae. albopictus, a mosquito of very plastic behaviour, is widespread throughout the island from sea-level to 2000 feet. It is a notable tree-hole breeder, but will breed freely on domestic premises in discarded tins and containers. When found breeding in tree-holes it shows a marked preference for the Mango tree (*Mangifera indica* L.); other favoured trees are the Flamboyant (*Delonix regia* Boj.), and the Papaya (*Carica papaya* L.). It is sometimes to be found breeding in small depressions in basaltic boulders.

It bites actively and persistently by day; rarely by night. It is an indifferent house frequenter and bites readily out of doors. In forested areas it can become a scourge. By general repute it is thought to be the vector of dengue fever in Mauritius.

The known larval predators of this mosquito are *Culex (Lutzia) tigripes* d'Emm. and certain small planarians.

THE ESTABLISHMENT AND MAINTENANCE OF THE COLONY.

A mass collection of larvae from natural breeding sites was made. Eggs obtained from the resulting adults were then used to found the colony.

From time to time, small larval collections have been added to prevent the formation of a genetically unsound strain by excessive inbreeding.

Eggs.

A little trouble was experienced at the outset, the gravid female preferring to affix her eggs to the sides of an enamel bowl. Eventually it was found possible to obtain the egg batches on damp filter-paper. The female was observed but once to oviposit directly on to a water surface.

Eggs laid on to the filter-paper were dried, and then stored for subsequent use. Such eggs were viable after 88 days of storage. None were viable after 100 days of storage.

Eggs of 1-12 hours in age gave a very uneven hatch. The cycle from larva to emerging adult was prolonged—batch 134, eggs of six hours in age, gave an

uneven hatch extending over four days ; adults emerged after 25 days. Mature eggs four to seven days old gave an even and almost immediate hatch.

Larvae.

Larvae of all instars were kept in the same enamel bowl. To the breeding water (rain water) was added a "soup", made of an infusion of grass and sugar-cane leaves. Proprietary breakfast foods have been used with success (e.g. "Bemax"). Extra care was necessary, as these foods encouraged the quick formation of a toxic bacterial surface scum.

Pupae were removed daily from the larval breeding bowls and up to 600 pupae were placed each day in the adult rearing cage.

Apparatus for the maintenance of fixed temperature and humidities were not available. The insectary's average temperature was 80° F., falling at night to a minimum of 56° F. Temperatures within the adult rearing cage were usually 2-3° F. higher than those of the insectary. The natural humidity within the cage was 80 per cent. R.H.

Adults.

The adults were housed in a large cage, 3' × 3' × 18'. The cage was constructed of plaster-board with wire gauze front and sides. Plaster board was used in preference to wood because local wood was unseasoned and cracked easily, and imported plywoods were too expensive. A cage of this size can accommodate several thousands of mosquitoes. Sleeved and hinged doors allow for the collection of adults and placing of the guinea-pigs.

The adult mosquitoes were fed on guinea-pigs. They were disinclined to feed on rabbits. They would feed avidly on the bared arm of human volunteers. The guinea-pigs were strapped into small cradles and placed in the cage for three to four hours each day.

Cotton-wool swabs soaked in sugar solution were not used because they tended to function as adhesive traps. Sliced bananas and split raisins were placed in the cage each day. Daily change was essential to prevent fungal growths.

Enamel saucers covered with a damp circle of filter-paper were placed in the cage to receive the eggs, which were later removed, dried and stored.

Predatory ants were deterred by placing the legs of the cage in tins containing water to which phenol had been added.

Life Cycle.

Emerging larva to emerging adult (from mature eggs) :

	Maximum (days).	Minimum (days).
1st instar-2nd instar .	2	1
2nd instar-3rd instar .	3	1½
3rd instar-4th instar .	3	2
4th instar-pupa .	3	2
Pupa-adult .	3	2
	—	—
	14	8½
	—	—

Gonotrophic Cycle.

From 1st blood meal to 1st oviposition . . .	3 days
From 2nd blood meal to 2nd oviposition . . .	2 ,,

SUMMARY.

A colony of *Aedes albopictus* has been maintained to provide substitute test-mosquitoes to replace *Ae. aegypti*, which may often be unobtainable due to eradication schemes.

The larvae were fed on an infusion of grass and sugar-cane leaves, or on "Bemax." The adults were fed on guinea-pigs or on man.

Notes on distribution, life cycle and gonotrophic cycles are presented.

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BIOLOGICAL NOTES ON SOME EAST AFRICAN AQUATIC HETEROPTERA

By H. B. N. HYNES, Ph.D., F.R.E.S.

(Department of Zoology, University of Liverpool).

DURING the years 1944-46, while travelling widely in Ethiopia, Kenya and Somalia, I spent some of my spare time collecting aquatic Heteroptera and making notes on their habitats.

I made collections at both high and low altitudes and in various types of habitat, and kept specimens of all the species found in each of the 74 localities studied. My collection was submitted to Professor R. Poisson of the Université de Rennes who very kindly named all the species for me and described several as new (1949, 1951). He has also read through the manuscript of this paper and offered useful comments. I wish here to tender my grateful thanks to him for this help.

My notes were made with the object of finding out something of the biology of the various species, of which little appears to be known. Almost all the papers that have been published on East African species of this group have been purely taxonomical studies. The only one I have found which contains any ecological information is that of Hutchinson (1930), which is based on a collection of Cryptocerata from southern Ethiopia.

I have found several species only once or a few times, and it is therefore not possible to infer much about these, but many were collected often, and examination of the records gives considerable information about types of habitat, differences between the habitats of species of the same genus, range of flight, etc. I have therefore felt it worthwhile to set down my findings despite their limitations. My data on the Gymnocerata are more extensive than those on the Cryptocerata because of the greater ease with which the former are observed and collected.

Most of the collection on which this paper is based has been presented to the British Museum.

LIST OF LOCALITIES.

The collections were made in three main regions. These were central and southern Ethiopia, in the general area described by Scott (1952), the high Kikuyu country north of Nairobi, Kenya, and the wide belt of low-lying hot dry country extending from Turkana in north-western Kenya across the Northern Province to Jubaland and Somalia. The Ethiopian and Kenya highlands are well watered, and streams and ponds are common. The lowlands are dry, and although a few permanent rivers and pools occur they are very widely scattered. During the short rainy seasons, however, temporary watercourses and pools become filled, and may remain so for many weeks.

In the following list the localities have been roughly classified into regions and types of habitat.

PROC. R. ENT. SOC. LOND. (A) 30. PTS. 4-6. (JUNE, 1955).

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ETHIOPIAN HIGHLANDS (central and southern Ethiopia).

Small Rapid Streams and Springs without Vegetation.

1. Addis Ababa, 2400 m., 1.i.1944, unshaded, stony.
2. Mullu, 9° 15' N., 38° 35' E., 2400 m., 23.i.1944, shaded limnocene.
3. Laleno river, 6° 30' N., 38° 20' E., 1780 m., 5.ii.1944, shaded, rocky.
4. Lenda river, 7° 14' N., 38° 37' E., 1920 m., 8.ii.1944, shaded, stony.
5. Maki river, 8° 10' N., 38° 50' E., 9.ii.1944, shaded, sandy, slightly polluted.
6. Tributary of Cabana river, 9° 5' N., 38° 48' E., 2700 m., 19.iii.1944, unshaded, rocky.
7. Caffo river, 9° 4' N., 38° 54' E., 2400 m., 26.iii.1944, unshaded, rocky.

Sluggish Streams Less than 5 m. Wide with Emergent Vegetation.

8. Mullu, 9° 15' N., 38° 35' E., 2400 m., 23.i.1944, unshaded, muddy.
9. Gidabo river, 6° 46' N., 38° 23' E., 1700 m., 4.ii.1944, shaded, rocky, swift in places.
10. Tributary of Gidabo river, 6° 44' N., 38° 22' E., 1700 m., 5.ii.1944, shaded, stony.
11. Tributary of Locke river, 6° 28' N., 38° 22' E., 1650 m., 6.ii.1944, unshaded, stony.
12. Tributary of Laleno river 6° 31' N., 38° 21' E., 1780 m., 6.ii.1944, unshaded, muddy.
13. Malao river, 6° 35' N., 38° 23' E., 1900 m., 6.ii.1944, shaded, muddy.
14. Shallo river, 7° 6' N., 38° 28' E., 1680 m., 3 & 7.ii.1944, shaded, muddy, aquatic vegetation.

Rivers More than 10 m. Wide with Aquatic or Emergent Vegetation.

15. Awash river, 8° 24' N., 39° 5' E., 1440 m., 1.ii.1944, unshaded, muddy, 60 m. wide.
16. Waracallo river, 7° 42' N., 38° 40' E., 1560 m., 3.ii.1944, unshaded, saline, 15 m. wide.
17. Bul Bula river, 7° 52' N., 38° 43' E., 1600 m., 2.ii.1944, shaded, reedy, 30 m. wide.
18. Suk Suki river (lower part of 17), 7° 43' N., 38° 38' E., 1525 m., 8.ii.1944, shaded, grassy, 30 m. wide.
19. Akaki river, 8° 52' N., 38° 48' E., 2070 m., 9.ii.1944, unshaded, weedy, 50 m. wide.

Lakes.

20. Lake Zwai at outflow, 7° 54' N., 38° 43' E., 1624 m., 2.ii.1944, wide swampy shore, aquatic vegetation.
21. Lake Langana, 7° 33' N., 38° 42' E., 1585 m., 3.ii.1944, open stony and sandy beach, slightly saline.
22. Lake Awasa, 7° 6' N., 38° 28' E., 1678 m., 3.ii.1944, open sandy beach, slightly saline.
23. Lake Awasa at inflow, 3.ii.1944, open weedy bay, probably fresh.
24. Lake south-west of Bole, 8° 22' N., 39° 2' E., 1550 m., 9.ii.1944, emergent and aquatic plants.

Permanent Ponds.

25. Addis Ababa, 2400 m., 1.i.1944, shaded, *Lemna* covered.
26. Cattle pool, 6° 43' N., 38° 20' E., 1700 m., 5.ii.1944, unshaded, emergent vegetation.

KENYA HIGHLANDS.

Rapid Stony Streams 1-2 m. Wide.

27. Ndarugu river, 0° 54' S., 36° 45' E., 2100 m., 18.ii.1945, shaded, emergent vegetation.
28. Limuru, 1° 8' S., 36° 38' E., 2190 m., 14.iv.1946, shaded, emergent vegetation.
29. Tributary of Karura river, 1° 10' S., 36° 43' E., 1950 m., 7.x.1944, shaded, emergent vegetation.

Sluggish Ditches and Channels, etc. 1-2 m. Wide.

30. Tributary of Kamiti river, 1° 10' S., 36° 55' E., 1500 m., 20.ii.1944, unshaded, stony slightly polluted.

31. Dyke, Ruiru, 1° 11' S., 36° 57' E., 1500 m., 20.ii.1945, unshaded, muddy, aquatic vegetation.
32. Catchment furrow, Nairobi M.C. dam, 1° 15' S., 36° 40' E., 2010 m., 26.ii.1945, unshaded, mossy concrete.
33. Tank, Limuru, 1° 8' S., 36° 38' E., 2190 m., 18.iii.1945, shaded, emergent grass, flowing water.
34. Dam outflow, Limuru, 1° 8' S., 36° 38' E., 2190 m., 14.iv.1946, shaded, emergent grass.
35. Furrow, Limuru, 1° 8' S., 36° 38' E., 2190 m., 15.iv.1946, shaded, emergent grass.
36. Tributary of Karura river, 1° 10' S., 36° 43' E., 1950 m., 7.x.1944, shaded emergent and aquatic vegetation.

Permanent Ponds and Dams.

37. Dam, Limuru 1° 8' S., 36° 38' E., 2190 m., 12.ii.1945, 18.iii.1945, 14.iv.1946, unshaded, emergent and aquatic vegetation.
38. Large dam, Ruiru, 1° 11' S., 36° 57' E., 1500 m., 20.ii.1945, unshaded, aquatic vegetation.
39. Small dam, Limuru, 1° 8' S., 36° 38' E., 2180 m., 16.iv.1946, shaded, emergent vegetation.
40. Quarry pool, Limuru, 1° 10' S., 36° 43' E., 1940 m., 18.iv.1946, shaded, aquatic vegetation.
41. Nairobi M.C. dam, 1° 15' S., 36° 40' E., 2010 m., 26.ii.1945, unshaded, aquatic vegetation.

LOW DRY COUNTRY (Kenya and Somalia).

Permanent Streams and Rivers.

42. Athi river, 2° 56' S., 38° 28' E., 540 m., 12.i.1945, 30 m. wide, sandy.
43. Tsavo river, 3° 0' S., 38° 28' E., 455 m., 12.i.1945, 5 m. wide, rocky and muddy, emergent vegetation.
44. Uaso Nyiro river, 0° 35' N., 37° 30' E., 930 m., 22.i.1945, 50 m., wide, muddy.
45. Irrigation dyke, Merca, 1° 45' N., 44° 45' E., 60 m., 13.ix.1945, 2 m. wide, emergent grass.
46. Irrigation dyke, Vittoria d'Africa, 1° 41' N., 44° 40' E., 30 m., 17.ix.1945, 3 m. wide, muddy, emergent grass.
47. Juba river, 2° 20' N., 42° 18' E., 116 m., 1.xi.1945, 100 m. wide, muddy.
48. Juba river, 0° 4' N., 42° 45' E., 9 m., 16.ix.1945, 100 m. wide, muddy.
49. Swamp, Mustahil (overflow of Webi Shebelli), 5° 14' N., 43° 45' E., 192 m., 28.x.1945, large swamp, aquatic vegetation.

Temporary Water-courses, "Wadis," Tree-lined, Open Sandy Beds.

50. Turkwell river, Kaputir, 2° 5' N., 35° 27' E., 1400 m., 12.viii.1944.
51. Turkwell river, Loiyapuya, 2° 25' N., 35° 22' E., 1300 m., 11.viii.1944.
52. Uaso Nyiro river, 1° 0' N., 39° 27' E., 195 m., 19.xi.1944.
53. Kikoko river, 2° 12' S., 37° 43' E., 1050 m., 10.i.1945, some permanent pools.
54. Webi Shebelli, 4° 45' N., 45° 13' E., 172 m., 21.v.1945, some permanent pools.
55. Webi Shebelli, 3° 52' N., 45° 35' E., 130 m., 20.v.1945.
56. Webi Shebelli, 2° 45' N., 45° 32' E., 109 m., 18.v.1946, some permanent pools.
57. Webi Shebelli, 2° 22' N., 45° 24' E., 104 m.

Permanent Pools.

58. Loiyapuya, 2° 25' N., 35° 22' E., 1300 m., 6.ix.1944, shaded, aquatic vegetation.
59. Sosoma, 0° 54' N., 38° 42' E., 510 m., 20.xii.1944, unshaded, no vegetation.
60. Kenani, 2° 48' S., 38° 16' E., 630 m., 11.i.1945, unshaded, aquatic vegetation.
61. Archer's Post, 0° 35' N., 37° 40' E., 810 m., 17.i.1945, partly shaded, no vegetation.
62. Rabable, 8° 17' N., 48° 22' E., 580 m., 10.xi.1945, unshaded, no vegetation.

Temporary Pools (approximate time since filling with water shown in brackets).

63. El Wak, 2° 50' N., 40° 55' E., 360 m., 16. xi. 1944 (4 weeks).
64. Habaswein, 1° 15' N., 39° 45' E., 225 m., 19. xi. 1944 (1 week).
65. Lolokwe, 0° 55' N., 37° 32' E., 900 m., 24. xi. 1944 (5 weeks).
66. Bur Wen, 3° 37' N., 45° 33' E., 126 m., 19. v. 1945 (1 week).
67. 4° 35' N., 45° 20' E., 195 m., 22. v. 1945 (2 weeks).
68. 4° 30' N., 45° 20' E., 210 m. (1 week).
69. 4° 6' N., 45° 35' E., 135 m., 22. v. 1945 (2 weeks).
70. 3° 44' N., 45° 35' E., 120 m., 22. v. 1945 (1 week).
71. Villagio, 2° 46' N., 45° 30' E., 108 m., 22. v. 1945 (3 weeks).
72. Mulla's pool, Galkayu, 6° 47' N., 47° 20' E., 280 m. (1 month).
73. Hodur, 4° 7' N., 43° 53' E., 51 m., 29. x. 1945. (4 weeks).
74. Tank, Hodur, 4° 7' N., 43° 53' E., 51 m., 29. x. 1945.

LIST OF SPECIES.

The numbers following each specific name show the localities in which each was taken.

Family GERRIDAE.

- Gerris gobana* Poisson, 2.7.8.
Gerris zuqualana Poisson, 19.25.
Gerris swakopensis (Stål), 7.9.12.14.17.30.31.33.34.36.37.38.39.41.
Gerris severini Kirkaldy, 23.38.
Limnogonus hypoleucus (Gerstäcker), 9.10.50.53.58.61.67.
Limnogonus leptocerus (Reuter), 42.43.44.45.46.47.49.52.58.60.61.63.64.65.67.
 68.69.71.73.
Tenagobonus (Tenagometra) hirsutus Poisson, 53.
Rhagadotarsus (Caprivia) hutchinsoni China, 53.
Eurymetra natalensis (Distant), 1.3.4.5.7.9.10.13.18.27.28.30.35.
Naboandulus patrizii Mancini, 48.49.54.55.56.
Hynesionella aethiopica Poisson, 16.17.18.20.

Family VELIIDAE.

- Tenagovelis sjoestedti* Kirkaldy, 18.30.31.43.53.
Rhagovelis nigricans (Burmeister), 5.9.15.16.17.18.30.44.51.
Rhagovelis infernalis africana Lundblad, 46.47.48.49.52.54.
Rhagovelis hynesi Poisson, 3.4.7.9.11.12.
Microvelis gracillima Reuter, 14.15.23.32.33.37.42.44.46.47.50.54.55.57.58.59.
 63.65.66.67.68.69.70.71.74.
Microvelis addisi Poisson. Gaforsa river, 9° 4' N., 38° 41' E., 2600 m., 26. xii. 1943.
Microvelis venustissima kenyalis Poisson, 27.35.36.39.
Microvelis awasai Poisson, 23.
Microvelis alluaudi Poisson, 4.5.9.29.44.65.
Microvelis kijabiensis Poisson, 33.35.36.39.
Microvelis noeli Poisson, 40.
Microvelis (Xyphoreloidea) major kilimandjaronis Poisson, 9.10.12.15.17.18.44.47.
 50.51.
Angilia schoutedeni Poisson, 31.

Family HEBRIDAE.

- Hebrus violaceus somaliensis* Poisson, 54.55.

Family HYDROMETRIDAE.

- Hydrometra albolineolata* Reuter, 9.31.44.47.50.51.60,

Hydrometra chopardi Poisson, 50.

Hydrometra somaliensis Poisson, 15.18.23.26.42.45.46.54.55.57.59.60.61.65.67.72.

Family MESOVELIIDAE.

Mesovelia vittigera Horvath, 9.12.15.17.20.23.24.26.30.31.36.37.38.41.43.44.45.
46.47.54.55.58.59.60.61.63.65.68.73.

Family NOTONECTIDAE.

Enithares chinai Jaczewski, 61.

Enithares glauca Bolivar, 6.7.8.

Enithares sobria Stål, 9.15.17.20.30.31.36.38.

Nychia marshalli (Scott), 19.38.

Anisops worthingtoni Jaczewski, 63.72.

Anisops debilis Gerstäcker, 50.58.62.65.

Anisops varia varia Fieber, 1.7.8.19.25.31.58.

Anisops sardea Herrich-Schäffer, 1.15.18.31.41.42.50.61.

Anisops (Micranisops) apicalis Stål, 20.43.

Anisops sp. (group *amaryllis* Hutchinson), 33.34.36.37.41.53.

Family PLEIDAE.

Plea (Paraplea) pullula Stål, 15.20.37.41.

Plea (Paraplea) piccanina Hutchinson, 47.48.

Family CORIXIDAE.

Micronecta (Basileonecta) scutellaris Stål, 15.20.22.23.24.31.38.

Micronecta (Basileonecta) dimidiata Poisson, 6.7.8.9.15.27.30.36.38.39.41.

Micronecta (Basileonecta) isis Horvath, 16.21.23.42.44.

Micronecta (Basileonecta) eupompe Hutchinson, 58.

Micronecta quewalepele Hutchinson, 54.

Agraptocorixa dakarica Jaczewski, 58.

Sigara (Tropocorixa) pectoralis (Fieber), 8.30.31.

Sigara (Tropocorixa) sexlineata Reuter (= *hedenborgi* Lundblad), 23.

Sigara (Tropocorixa) omercooperi Hutchinson, 2.26.

Sigara (Tropocorixa) serpentis Hutchinson, 1.

Sigara (Tropocorixa) hoggarica Poisson (= *brevixypha* Brown), 7.

Pseudoglaenocorixa hugoscotti (Hutchinson), 1.6.7.8.

Family NAUCORIDAE.

Naucoris obscuratus Montandon, 7.

Laccocoris limigenus Stål, 9.17.20.21.23.30.62.

Macrocoris nigropunctatus Montandon, 36.37.

Family BELOSTOMIDAE.

Hydrocyrius columbiae Spinola, 20.

Lethocerus cordofanus Mayr, 43.60.

Sphaerodema grassei Poisson, 14.15.16.17.20.23.24.30.31.38.51.58.61.

Family RANATRIDAE.

Ranatra parvipes vicina Signoret, 17.20.24.

Ranatra bottegoi Montandon, 9.37.72.

Family NEPIDAE.

Laccotrephes brachialis brachialis Gerstäcker, 1.6.7.10.37.

Laccotrephes calcaratus Montandon, 58.

Laccotrephes ater steindachneri (E. Ferrari), 14.

NOTES ON BIOLOGY.

Family GERRIDAE.

Several of the species were taken only a few times. *Gerris gobana* was found only on two small streams and a spring-pool in high country in Ethiopia; the species was originally described from this region (Poisson 1940); all the specimens were apterous. Similarly *G. zuqualana* was found abundantly on a *Lemna*-covered pond and sparsely amongst emergent vegetation on still water by a river-bank; both winged and apterous specimens were collected. This perhaps indicates a habitat difference between these two species, which occur in the same general area. *G. severini* was found only on two widely separated upland lakes, where it was confined to areas where the water-surface was broken by *Potamogeton* leaves; both winged and apterous specimens were present. These three species occurred singly or in loose shoals. *Tenagogonus hirsutus* and its form *reductus* (Poisson 1949), and *Rhagadotarsus hutchinsoni* were found only once on pools in an almost dry water-course. The former occurred singly on large clear shaded pools, over which it ran with astonishing swiftness; all the specimens seen were apterous. The latter was confined to one very small open muddy pool, where hundreds were crowded together. Many were feeding on drowning Jassidae, and all were apterous apart from one female, which was fully winged. No nymphs were present, and a few days later the pool was dry and the bugs had disappeared.

More information is available for the other species.

Gerris swakopensis was found many times at altitudes over 1500 m. in the highlands of Kenya and Ethiopia. All the habitats where nymphs and apterous specimens were found were still or very slowly flowing water, and in nearly all these localities winged adults were present also. On the few swift-flowing streams where the species was collected only scattered winged adults were found. The insects occurred either singly or in loose shoals. It would seem that the species spreads readily by flight, and that winged adults may alight temporarily on water that is too fast-flowing for breeding.

Limnogonus hypoleucus was taken in seven varied localities. Nymphs and apterous adults were found only on heavily shaded permanent pools at medium altitudes (1050-1300 m.), and on these winged specimens also occurred. Small numbers of winged adults were also taken on slow streams up to 1700 m. and on varied localities down to quite low altitudes (195 m.). The specimens occurred singly and were invariably confined to the shade. This species, therefore, apparently breeds only on still shaded water at medium altitudes, but the winged forms range widely. No evidence of breeding was found at low or high altitudes.

L. leptocerus was found only at altitudes below 1400 m. There it was very common and occurred along the banks of rivers, on irrigation dykes, wadis and temporary pools. The insects did not form shoals even when large numbers were present. Remarkable features of this species were that in the dry country it was found on puddles and temporary pools within a few days of their filling, and that, unlike any other Gerrid I have collected, it flew readily from the water surface when pursued. All but one of the specimens seen were fully winged; the one being a female taken *in copula* with a winged male on a permanent irrigation dyke. Mating pairs were often seen on temporary pools. It would

seem that the species maintains itself on permanent water and flies far and wide over the dry semi-desert at the onset of the rains, and may breed successfully on temporary pools. Some of the pools on which it was found were over 80 km. from permanent water, so individuals must be able to travel a long distance. It seems possible that the passage of the large strato-cumulus rain-clouds induces the bugs to fly and that they travel with them, and so arrive where the scattered rain falls. It seems fairly certain that no specimens can survive on the sites of the temporary pools during the dry weather, as all water-bugs, including this species, succumb rapidly in a dry atmosphere: presumably therefore flight can only occur during the rains. It is equally certain that the bugs do not survive the dry season as eggs, because the first specimens to appear on temporary water are always winged adults. The insects occurred individually or in pairs on the open water, which in shallow pools was often very warm in the sun, and were seen to feed on drowning insects. Jaczewski (1926) reports finding only winged specimens and nymphs on pools in the steppe near Dakar, whereas about half the specimens in a large collection from pools and canals in Egypt were apterous (1936). This supports the suggestion made above that apterous specimens are probably only produced on permanent water.

Eurymetra natalensis was found abundantly on running water at altitudes of more than 1500 m. All the localities were more or less shaded, and most were small streams, although one was a fairly large river. All the specimens seen were apterous and nymphs were always present. The insects occurred in small groups in various stages of development, and were very difficult to catch because of their speed. Kirkaldy (1910) records winged specimens from the Kilimanjaro area. Esaki (1928) states that this species is found on stagnant water in South and East Africa; I never found it in such a habitat.

Naboandalus patrizii was found only on the Juba river and its tributary the Webi Shebelli. Both these rivers flow from south-eastern Ethiopia across dry semi-desert country. The Juba is permanent, but the Webi Shebelli is dry for long periods, although there are, at intervals along its course, areas of swamp where there are always pools. *N. patrizii* occurred in large shoals on the turbid waters of these rivers. The insects remained under the shade of trees and bushes during the day, and spread out over the water at dusk, where they remained until dawn. Nymphs and adults occurred together in the shoals, which were always quite separate from those of *Rhagovelia*, and many specimens were observed feeding on drowning insects. Large shoals were observed on temporary reaches of the Webi Shebelli many miles from permanent water. Poisson (1949) described the specimens in my collection as a new form (*hynesi*) of the species, from the original description of which they differ in a few small characters. Mancini (1939) described the species from the river Bubasc in Jubaland. This lies about 150 km. south-west of the mouth of the Juba, from which it is separated by semi-desert country. Many thousands of form *hynesi* were seen, and amongst these only a single winged specimen was observed. This rarity of alate forms and the formidable barrier of dry country between the two river systems probably results in little opportunity for crossing between the two populations, and may account for the differences between the two forms.

Hynesionella aethiopica was found only in the Lake Zwai region of the Ethiopian rift valley. It was common and breeding on Lake Zwai itself and its outflow, and on the Warracallo river, which flows from Lake Langana to

Lake Hora Abgiata. The Suk Suki river flows from Lake Zwai into the latter. Both the lower lakes and the Waracallo river are saline. The insects were common, and nymphs were present at all the points where the species was seen. The bugs occurred singly, and ran with great speed.

From the data given above it seems that in this family some species, e.g. *G. gobana*, *N. patrizii* and *H. aethiopica* are confined to quite small areas whereas others, e.g. *L. leptocerus* and *E. natalensis*, are to be found over large regions. Each species seems to occur, or at any rate to breed, only in certain types of habitat. The apparent correlation of the occurrence of some species with altitude may be connected with temperature, but it is just as possible that suitable habitats are only found at certain altitudes.

Family VELIIDAE.

Some species were collected only once, so little can be said of their habitat preferences. Several species were, however, collected several times.

Tenagovelia sjoestedti was found breeding, as shown by the presence of nymphs and apterous specimens, only on slowly moving water at fairly high altitudes (c. 1500 m.) in Kenya and Ethiopia. Elsewhere only winged specimens were found; these localities were a drain and a pool in a dry river. Two isolated apterous specimens were found on the Tsavo river at 455 m.: possibly these had been carried down from higher altitudes by flood-water. The insects occurred in loose groups, and in general habits seemed to resemble European species of *Velia*.

Rhagovelia was represented in my collections by three species. *R. nigricans* was found commonly on slow-flowing water in the highlands of Kenya and Ethiopia at altitudes between 930 and 1700 m. *R. hynesi* was found commonly on fairly swift-flowing water in the Ethiopian highlands at altitudes of 1650 to 2400 m. On one stream, No. 9, both species were found. *R. infernalis africana* was only found at altitudes below 200 m. where it occurred both on permanent and temporary rivers. It is interesting to note that on the Uaso Nyiro river at 930 m. *R. nigricans* was found, while at 195 m., where the river is temporary, only *R. i. africana* occurred. It would seem that in this genus in East Africa, as I have earlier shown to occur in Trinidad (Hynes, 1948), each species occupies a well-defined zone, and they do not normally occur together. The locality where both *R. nigricans* and *R. hynesi* were found was near both their altitudinal limits, and areas of both fast and slow-flowing water were present. A point of some interest is that I found no specimens of *Rhagovelia* on high streams in Kenya, where one might have expected to find *R. hynesi* or another species occupying the same niche. It is perhaps relevant to note here that whereas both winged and apterous specimens of *R. nigricans* and *R. i. africana* were collected, only apterous specimens of *R. hynesi* were seen. If alate specimens of this species do not exist, or are very rare, it is possible that it is confined to the Ethiopian highlands. All three species occurred in loose shoals of individuals all in the same stage of development. This segregation of the instars was also observed in shoals of several species of this genus in Trinidad.

Five species of *Microvelia* were collected several times. *M. venustissima* and *M. kijabiensis* were found only amongst emergent vegetation beside shaded flowing water at high altitudes (over 1950 m.) in Kenya, where both winged

and apterous specimens occurred. (*M. addisi* was found in a similar habitat in Ethiopia on the one occasion on which it was taken.) *M. alluaudi* was found in similar localities, but at lower altitudes, in Kenya and Ethiopia. All the specimens were apterous except one, which was found on a temporary pool at 900 m. *M. major kilimandjaronis* was found at similar altitudes in Kenya and Ethiopia, but apparently tended to occur on larger rivers and unlike *M. alluaudi* was not found beside swift-flowing water. It was found down at a low altitude in Somalia and was breeding on the Turkwell river 80 km. downstream of permanent water. In this species winged specimens were found only at altitudes below 1400 m. Only apterous specimens were seen at higher altitudes, and at the lowest point at which it was collected all the specimens were macropterous.

The most interesting species of this genus encountered was *M. gracillima*. This small species was found frequently and on very varied types of habitat. At high altitudes (over 1600 m.) in Kenya and Ethiopia both apterous and macropterous specimens were found on slow streams, ditches and lakes, where they occurred amongst vegetation. At lower altitudes, down almost to sea level, only fully macropterous specimens were found. These occurred on both permanent and temporary rivers and pools and, like *Limnogonus leptocerus*, the species appeared on temporary pools very far from permanent water soon after rain. Copulating pairs were seen on several such pools, and on some very large numbers of insects were present within a few days of rainfall. Unlike *L. leptocerus*, the insects did not fly off the water when disturbed, but hid in any available cover. It would seem that this species ranges far out into semi-desert country in the rainy season and may succeed in breeding on temporary waters. It is astonishing to have evidence that such small insects can travel distances of at least 80 km., even though they may be aided in their flight by turbulence under rain-clouds. It may be noted here that Jaczewski (1926 and 1936) also found only winged adults of this species at low altitudes near Dakar and in Egypt.

From the above notes it would appear that in this genus, as in *Rhagovelia*, each species tends to occur in a definite type of habitat, and there appears in some species to be a correlation between altitude and the development of wings. This is possibly the result of temperature or rainfall, which, generally, vary with altitude. In *M. gracillima* the production of apterous specimens at low altitudes would of course result in their elimination from the temporary waters.

Family HYDROMETRIDAE.

Only a single specimen of *Hydrometra chopardi* was taken, on a temporary water course. *H. albolineolata* and *H. somaliensis* were both collected several times. There were no obvious ecological differences between the habitats of the two species, but they were not found together. *H. albolineolata*, all specimens of which were winged, was found on a pond at 630 m., and on several rivers from 1700 m. down to 116 m., and was twice found on temporary parts of the Turkwell river. *H. somaliensis* was found in various types of locality (ponds, dykes, permanent and temporary rivers, etc.) and was once found commonly on a temporary pool. Most of the specimens were fully winged, but a few brachypterous specimens were found on permanent water, and one

specimen, from the temporary pool, to which it must have flown, had wings about three quarters of the full length.

Family MESOVELIIDAE.

Mesovelia vittigera was collected in a wide variety of habitats containing still or slowly flowing water, and over a wide range of altitude. The bugs were most common where leaves of water-lily or pond-weed broke the surface, or where there was dense emergent herbaceous vegetation. Apterous specimens were found only in such habitats. Winged specimens usually occurred together with apterous ones, but were also found singly or in small numbers, in other types of habitat, including temporary pools far from permanent water. Many of the winged specimens had mutilated wings, a phenomenon which has been discussed by Poisson (1933), and I observed that it occurred even on temporary pools. It is very improbable that specimens lacking the membrane and often the clavus also, can fly, so these specimens would be unable to leave again.

This species presumably flies readily and may breed in many types of habitat, but production of apterous individuals, and possibly of nymphs also is somehow controlled by the presence of vegetation. Only at station 65, a permanent rocky pool without vegetation, were nymphs found in the absence of apterous adults; elsewhere where only winged adults were collected nymphs were never seen, although winged adults were often seen *in copula*.

Family NOTONECTIDAE.

My collection gives little information about the habitats of species of this family as most of them were collected infrequently. There appears to be a distinction between the types of habitat in which *Enithares glauca* and *E. sobria* occur. The former was found only in small stony streams at high altitudes in Ethiopia (2400–2700 m.), and a nymph probably of this species was taken in a similar locality (No. 27) in Kenya. *E. sobria* was found in several types of locality, including lakes, rivers and ditches, but all with vegetation, and at lower altitudes (1440–1950 m.). Hutchinson (1930), however, records *E. glauca* from ponds as well as streams in the Ethiopian highlands.

Anisops worthingtoni, which Jaczewski (1933) described from Lake Rudolf, in the extreme west of the region covered by my collection, was twice found in large numbers in temporary pools in Somalia. *A. debilis* was found in large numbers only in two permanent pools in the dry country, although single specimens were taken in two other habitats. *A. varia varia* and *A. sardea* were also found only in permanent water but at high as well as low altitudes, and in three localities they were collected together. From these meagre data little can be inferred, but it seems clear that *A. worthingtoni* flies readily. Hutchinson (1930) noted with surprise the absence of *A. varia varia* from collections from central Ethiopia, but, as I found it several times near Addis Ababa, it would seem merely to have been overlooked.

Family CORIXIDAE.

Most of the species in this family were collected only occasionally, but some points of interest arise.

Micronecta scutellaris and *M. dimidiata* appear to differ in their altitudinal ranges. The latter was found at altitudes from 1500–2700 m., thus ranging

considerably higher than the upper limit of 8000 ft. (2400 m.) suggested for most species of this genus by Hutchinson (1930). All the localities were running water or closely associated with it. *M. scutellaris* was found only at lower altitudes (1440–1678 m.), and the highest locality, Lake Awasa, where it was abundant, is saline. It occurred only in clear open water with a muddy substratum.

At high altitudes in Ethiopia *M. isis* was found only in slightly saline waters (Lake Langana and its outflow, and the inflow of Lake Awasa). It was absent from the more saline waters of Lake Awasa itself, where it was replaced by *M. scutellaris*: it was absent also from the quite fresh water of the inflowing river. At lower altitudes, below the apparent limit of *M. scutellaris*, it was found in two permanent rivers in Kenya. It would seem possible that in this genus the species tend to occupy different types of habitat, and that these vary with altitude.

Pseudoglaenocorixa hugoscotti, which Hutchinson (1930) recorded only from tributaries of the Blue Nile, was found in three tributaries of the Awash river, which flows eastwards. All three stations were, however, in the high country near Addis Ababa, and so not far from the tributaries of the Nile.

Family NAUCORIDAE.

Of the three species collected two were found only once and twice respectively. *Naucoris obscuratus* was common and breeding in a high rocky stream near Addis Ababa, and *Macrocoris nigropunctatus* was found in two high weedy habitats near Nairobi, in one of which it was breeding.

Laccocoris limigenus was found only at lower altitudes, below 1700 m., in still or slowly moving water, and was almost always amongst aquatic vegetation. It was, however, abundant on the bare sandy and stony shore of Lake Langana, the waters of which are slightly saline, although just drinkable. Here the littoral fauna appeared to consist only of this species, a few Libellulid nymphs and Hydroporine beetles, and vast numbers of *Micronecta isis*. Presumably the *Micronecta* formed the chief food of the *Laccocoris*.

Little can be inferred about the habitats of the HEBRIDAE, PLEIDAE, BELOSTOMIDAE, RANATRIDAE, and NEPIDAE as the species were taken infrequently. *Plea* spp. and most BELOSTOMIDAE were found only where there was vegetation. Amongst the latter *Sphaerodema grassei* was collected fairly frequently at altitudes of over 800 m., and all the localities were still or slowly flowing water. Several males were found with eggs attached to their wings.

Amongst the NEPIDAE, *Laccotrephes brachialis* was found only in streams and a stream dam all at high altitudes (over 1700 m.), whereas *L. ater* and *L. calcaratus*, although both found only once, were taken at lower altitudes.

Ranatra bottegoi is of some interest as a specimen was collected at station 72, the Mulla's Pool, Galkayu. This specimen would appear to have flown a considerable distance. The pool lies in a large pit, possibly of meteoric origin, which is at least 100 km. from permanent water. It fills rarely, although when it does the water persists for a long time and a large fauna of Anostraca appears. When the specimen was collected the pool had filled to a depth of about 10 m. a month earlier. Previously it had been dry for two years. Mancini (1939) states that this species is exclusively Somalian, but I found it also in

the highlands of Kenya and Ethiopia, where, like *R. parvipes vicina*, it was found only amongst vegetation.

CONCLUSIONS.

This study shows that, as might have been expected, it is possible to define in general terms the type of habitat in which many species of water-bug occur in East Africa. It is also possible to show that within several genera each species occupies a different type of habitat. I have been unable to find that anyone has before attempted to define the types of habitat of the various species in this region.

Perhaps the most striking result of this work has been the demonstration that several species of skaters, e.g. *Limnogonus leptocerus*, *Microvelia gracillima* and *Mesovelia vittigera*, fly very great distances over dry semi-desert country during the short rainy season, and are more or less regular inhabitants of temporary pools.

It would also seem that some of the Cryptocerata, e.g. *Anisops worthingtoni* and *Ranatra bottegoi* are able to fly long distances in the dry country which covers large areas of East Africa.

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LARVAE OF THE BRITISH TRICHOPTERA—50–51.

By N. E. HICKIN, Ph.D., F.R.E.S.

50—*Phryganea obsoleta* McLachlan.51—*Phryganea striata* L. (Phryganeidae).*P. obsoleta*.

I FIRST collected the adults of this species in 1938 at Grisedale Tarn near Dolly Waggon Pike, Westmorland, at a height of 1768 feet. I secured also a number of larvae. They were very common, and quite conspicuous as they walked over the submerged sphagnum and shoreweed (*Littorella uniflora*). Some further larvae from Scandale Tarn at 1820 feet were obtained where Mr. D. E. Kimmins had collected adults in 1941. Then on 22nd August, 1953, I found this species in great profusion in and around Llynhillan, Radnorshire. This lovely lake is 1243 feet above sea level, it is nowhere more than a few feet deep and *Littorella uniflora* grows everywhere in it. During the subsequent few days, although a strong wind was blowing in this rather exposed situation, specimens of all life stages of *P. obsoleta* were collected. On 23rd August a considerable emergence took place, commencing about 10 a.m. It was a fine day, windy but warm, and several thousand adults were seen making their way to the edge of the lake, skating on the surface of the water, and very reminiscent of the swimming pupa. From noon to 3.30 p.m. many pairs were seen on the rushes at the lake edge, and it was noticed that apparent virgin females exuded a small bead of greenish fluid from the abdomen. The fluid was very sticky, and if it got transferred to the wings of the collected insects it made the setting operation very difficult, by gluing the wings to the boards. Later on the same day the weather deteriorated, it became very cold and very windy, and the *P. obsoleta* adults sheltered deep in the centre of the rush tussocks, in company with adults of *Cyrtus flavidus* McLach. and *Limnephilus vittatus* F. and a few very late *Trienodes bicolor* Curt. Egg masses of *P. obsoleta* were found commonly in the lake around the margin on 31st August.

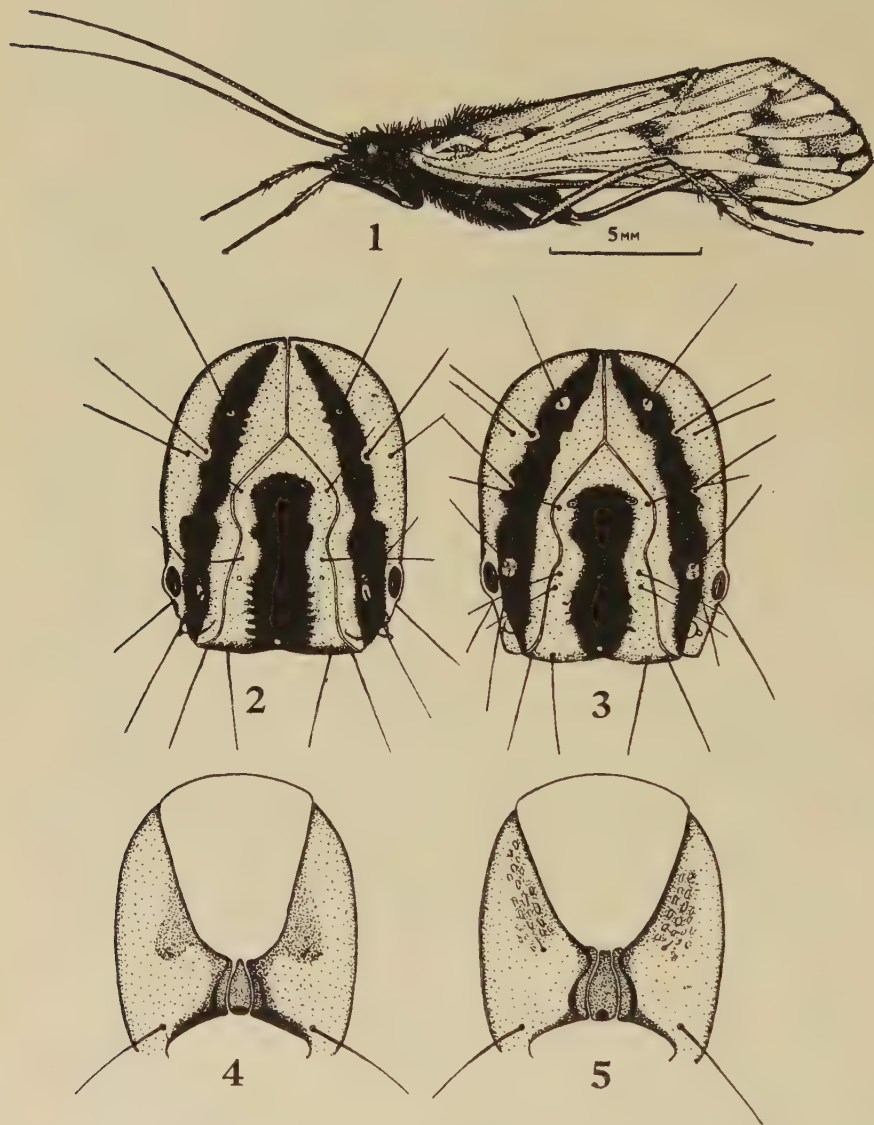
The wings of the freshly emerged adults have a milky appearance, and it is not until the day after emergence that the milky appearance is lost and the wings assume a brownish tinge.

P. striata.

Larvae of this species were collected from Clay Pond near Wray Castle, Lake Windermere, in 1945. They are very common in this small pond, and, in addition, larvae have been collected in many other lakes, ponds and sluggish streams near Lake Windermere. When I made my description of the larvae of *Phryganea grandis* L. I included amongst my material some half-grown larvae which I now know to have been *Phryganea striata*. However, no characters given in my paper on *Phryganea grandis* were erroneous.

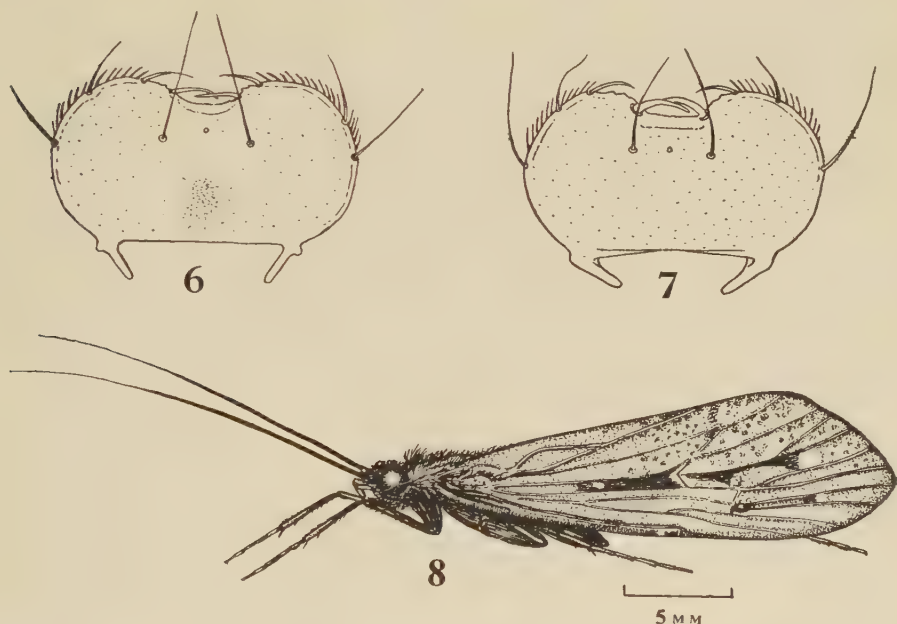
PROC. R. ENT. SOC. LOND. (A) 30. PTS. 4–6. (JUNE, 1955).

For my descriptions of larvae of the genus *Phryganea*, of which this paper is the completion, further undoubted *Phryganea grandis* have been collected from Welford-on-Avon, Warwickshire, and studied. More larvae of *P. striata* were collected from a pool at Nutley, Ashbourne Forest, Sussex, one of which was reared to the adult stage, a female emerging on 10th June, 1953.



FIGS. 1-5.—*Phryganea obsoleta*; (1) Adult, lateral view. Head of larva (2) anterior aspect; (4) ventral aspect; mouthparts omitted. *Phryganea striata*; Head of larva (3) anterior aspect; (5) ventral aspect, mouthparts omitted.

Larva of *Phryganea obsoleta* very like that of *P. grandis*, *P. varia* and *P. striata*. Length 25 mm., width 4 mm. Case length 28-35 mm., width 4.5 mm. Formed spirally with cut pieces of shoreweed, leaves or pieces of vegetable debris. Head very like that of *P. striata* L., examination of figs. 2 and 3 will, however, show several rather small differences. In the case of *P. striata* the black band in the clypeus narrows almost to a point at the oral margin, but in *P. obsoleta* the black band does not narrow and the oral margin of the clypeus is much darker. From beneath, the oral margin of the genae is black and is continuous with two wing-like dark marks extending to the aboral margin of the genae. The muscle-spots are barely discernible in *P. obsoleta* but are readily seen in *P. striata*. *Abdominal gills*.—All larvae of the British species of *Phryganea* have long filiform gills. In *P. obsoleta*, *P. striata* and *P. grandis* there are two gills on each side of the first abdominal segment, then on the second to the seventh segments there are six gills on each side, and in the case of *P. grandis* and *P. obsoleta*, on the eighth segment there are two gills on each side; in *P. striata* there are three on each side. A number of *P. obsoleta* were collected from Llynhillan on 23rd August, 1953. Two of these larvae, kept in an aquarium, measured 23 mm. in length on 13th February, 1954, whilst larvae hatched from an egg mass collected from Llynhillan on 23rd August, 1953, were only 11 mm. in length at the same time. It thus seems certain that two years are spent in the larval stage.



FIGS. 6-8.—Labrum of larva of (6) *Phryganea obsoleta*: (7) *Phryganea striata*. (8) *P. striata*. Adult, lateral view.

SUMMARY.

The larvae of *Phryganea obsoleta* McLachlan, and of *P. striata* L. are described and figured, and figures of the adults given.

PROC. R. ENT. SOC. LOND. (A) 30. PTS. 4-6. (JUNE, 1955).

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MIGRATION OF BUTTERFLIES IN ARGENTINA, 1953-54.

By KENNETH J. HAYWARD, Hon. D.Sc., F.R.E.S., F.R.G.S., F.Z.S.

(*Institute of Entomology, University of Tucumán.*)

THE following observations on migration of butterflies in north-western Argentina refer principally to an extensive movement of *Ascia monuste* (L.), forma *automate* (Burm.), that took place during the late spring and early summer of 1953-54, to which I have, for the sake of record, appended one or two other isolated observations on migration of *Libytheana carinenta* (Cr.).

Both these species are well known migrants and I have little doubt that their migratory flights are annual, but there are years when these are on so small a scale that in a country so vast and so thinly populated, they may well escape notice. In the case of *monuste*, these migrations occasionally reach almost unbelievable proportions and two such flights I have described elsewhere (1931 and 1953).

I have employed sun time throughout the following notes, and the figure in brackets following wind direction refers to the strength on the Beaufort scale. All references are to the city of Tucumán.

April 6th, 1953.—Great numbers of *Libytheana carinenta* suddenly appeared in the city of Tucumán following a severe dust storm that blew in from the south during the late afternoon. They were to be seen everywhere, resting on walls and windows and even invaded the houses. This species had not been present before this date.

April 9th.—*Libytheana carinenta* was observed flying north between 1 and 2 p.m. at heights varying from 4 to 15 ft. The wind was light westerly, but later became gusty reaching force 2 (Beaufort scale).

Dec. 7th.—Great numbers of *Ascia monuste* suddenly made their appearance at 11 a.m. The wind was east, veering later towards the west, force 1. These butterflies remained to feed.

Dec. 8th.—At 6 a.m. *monuste* was already feeding, and half an hour later the butterflies began to rise and fly west. I left Tucumán at 8 a.m., going north for 20 miles, and throughout this trip they were passing west at about 20 ft., flying towards the mountains some 10 miles to the west. At the village of Tapia I turned west for 15 miles till I reached Raco. Along this road the *monuste* were flying in a more southerly direction. At Raco, a village lying in a narrow valley giving access to the western valleys behind the first range of mountains, *monuste* were passing south in countless millions before a following wind, maintaining a steady 25-30 ft. above the ground whatever its contour. Suddenly, at about noon, the flight flattened out for no apparent reason, the butterflies coming down to a maximum height of about three feet, still hugging the contours, till at 1 p.m. they practically ceased to pass. It was not possible to calculate the wind velocity owing to the nature of the surroundings, but the speed of flight was 25 m.p.h. In the late afternoon very severe thunderstorms began to arrive from the north, accompanied by heavy rain.

Dec. 9th.—At 6.30 a.m. the small ground population of *monuste* in Tucumán were already beginning to rise and fly north, the wind being light westerly. Shortly afterwards *monuste* were observed at about 200 ft. *drifting* northwards, and they continued to do so till 5 p.m. when the wind was S. (1). The numbers were never great, but several were always in sight at any given moment.

Dec. 10th.—At noon *monuste* flying at between 100–200 ft. began to cross Tucumán from the east, flying indecisively at first and later at a faster rate. Wind NE. (2) but falling away. At 3 p.m. a few butterflies were still going over, flying very fast and apparently at about 300 ft.

Dec. 11th.—Wind S. at noon and SSW. at 3 p.m., lessening in strength from 2 to 1. At 6 a.m. a few *monuste* were here and there spiralling upwards to about 100 ft. where for over an hour they hung about as though waiting a signal to depart. Between 11 and 11.30 a small swarm passed, flying south against the wind at between 100–150 ft. During mid-afternoon *monuste* were observed flying in the opposite direction in small numbers at about 150–200 ft. After dark (8.30 p.m.) the streets became full of tired butterflies that seemed almost incapable of further effort. Half an hour later the city was suddenly swept by a hurricane of wind, rain and hail, and all exposed butterflies must have perished.

Dec. 12th.—Occasionally a few *monuste* could be seen *drifting* north on a light wind at a very great height.

Dec. 13th.—After a night of rain, *monuste* were seen *drifting* a little east of north on a light wind. They were at approximately 300 ft. and appeared to be completely wind borne. They continued to pass from 10 a.m. till dark, when some began to flutter down to sleep.

Dec. 14th.—At 8.30 a.m. *monuste* began to drift overhead at 300 ft., going towards the north east, the drift ceasing at 10 a.m. At 10.30 a small swarm passed overhead, coming in very low from the west. From 5 p.m. till dark *monuste* flying in considerable numbers from ground level up to about 100 ft. arrived from the west and settled. The day was calm, without appreciable wind.

Dec. 15th.—Wind SSE. (2), sunny till 3 p.m. and later overcast. At 10.30 a.m. *monuste* were observed flying north at 150 ft. Although never in great numbers a steady stream was maintained till 3 p.m., after which they began to thin out. At noon another flight with a density of about 400 per minute on a 100-yard front moving at heights varying from 10–60 ft. passed, travelling very fast from west to east. This flight continued till 3 p.m.

Dec. 16th.—Wind SSE. (1), sunny till 12.30 after which cloudy. At about 11 a.m. a swarm of *monuste* passed flying very fast between ground level and 150 ft., whilst above this height some were seen *drifting*. The density of the swarm diminished proportionally to the height of flight.

Dec. 17th.—Wind SE. (1), sunny. At 11 a.m. *monuste* flying between ground level and 60 ft. began to arrive from the west and continued to pass at a fast rate until 12.30, after which stragglers were seen till 2 p.m. About noon many butterflies at about 100 ft. were observed “playing” or drifting around, showing a tendency to proceed in a southerly direction. Perhaps another swarm?

Dec. 18th and 19th.—Bad weather, no *monuste* seen.

Dec. 20th.—Wind E. (1). Between 10-11 a.m. a small flight of *monuste* flying very low amongst the trees and houses passed west to east whilst at a great height an occasional specimen was observed *drifting* south.

Dec. 21st.—No movement observed.

Dec. 22nd.—Wind SW. (1). From 11 a.m. till 1 p.m. a fairly constant stream of *monuste* flying from ground level up to 50ft. passed towards the east, after which stragglers continued to do so till 4 p.m. One or two *Phoebis sennae* (L.) accompanied this flight.

Dec. 23rd till 25th.—No movement observed.

Dec. 26th and 27th.—Wind S., light. Throughout both days a few odd specimens of *monuste* were observed flying in an easterly direction at between 10-40 ft. Although a steady stream was maintained, there were never more than two or three specimens in sight at any given moment.

Dec. 28th.—No movement observed.

Dec. 29th.—Wind SE. (1). During the morning *monuste* were flying north at heights between 15-40 ft., never more than two or three in sight at once. A few *Libytheana carinenta* were observed flying east between ground level and 10 ft. accompanied by an occasional *Junonia evarete* (Cr.).

Dec. 30th till Jan. 2nd, 1954.—No migratory movement observed.

Jan. 3rd.—Wind E. (1). Between 11 a.m. and 2 p.m. a flight of *monuste* reaching up to 100 ft. passed going north, twenty to thirty specimens being always in sight.

Jan. 4th.—Wind E. (1), veering later to S. and becoming stronger after midday. At 11 a.m. *monuste* commenced to pass, going north with a density that at times reached 60-100 individuals per minute on a 100-yard front though generally far fewer. They were flying at 20-100 ft., though the last individuals observed (that passed at about 2.30 p.m.) were at 150 ft.

Jan. 5th till 7th.—No movement observed.

Jan. 8th.—Wind S., very light. Throughout the day a few *L. carinenta* were observed flying west at between 10-15 ft., passing in small bands or waves. Very occasionally an odd *monuste*, *Colias lesbia* (F.) or *Junonia evarete* accompanied them. Between 12.30 and 1 p.m. a small swarm of *monuste*, going fast, passed in the same direction.

Jan. 9th.—Wind S. (1). At 10 a.m. *monuste* began to pass flying south at heights between 6 and 20 ft., accompanied by a few *carinenta* and odd specimens of *Colias lesbia*, *Junonia evarete* and *Eurema deva* (Dblly.). The flight was of short duration.

Jan. 14th.—Wind E. (1). During mid-afternoon there was an infiltration of *monuste* from the south that built up a considerable ground population which disappeared the following morning. This was the first fine period after several days of rain.

Jan. 16th and 17th.—Wind N., light. During the morning *monuste* flew east in small groups, there being frequent intervals when none were to be seen.

Jan. 18th.—Wind E. (1). From mid-morning till late afternoon *monuste* could be observed flying east in swathes that at times reached a density of

300 individuals per minute on a 100-yard front and between which only a few specimens were to be seen. The height of flight lay between 15-20 ft.

Jan. 19th.—Wind N. (1). *Ascia monuste* continued to pass as on the previous day, but in lesser numbers. They appeared weary.

Jan. 20th.—A few *monuste* continued to straggle towards the east against a light breeze. After this date no further migration was observed.

SUMMARY AND CONCLUSIONS.

During the late spring and early summer of 1953-54, a number of migratory flights of *Ascia monuste* (L.) and occasional flights of *Libytheana carinenta* (Cr.) came under the observation of the author and are here recorded. All these flights took place in the neighbourhood of the city of Tucumán.

The behaviour of the butterflies during these migratory flights confirmed in every respect the conclusions reached by the author after due study of similar flights during 1951-52, which will be found set out in Vol. 28 of these *Proceedings* (page 73) and need not be here repeated. The speed of 25 miles per hour attained by *Ascia monuste* during the flight recorded for December 8th was due to a very strong following wind.

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REMARKS UPON THE MALE AND FEMALE GENITALIA AND ABDOMEN OF ARADIDAE (HETEROPTERA).

By DENNIS LESTON, F.R.E.S.

INTRODUCTION.

REUTER (1912) considered the superfamily Aradoidea (as Aradoideae) to comprise two families, Aradidae and Dysodiidae; subsequent authors have added Termitaphididae, a peculiar family of termitophiles. Recently Leston, Pendergrast and Southwood (1954) have attached this superfamily to their series Pentatomomorpha on the morphological similarities displayed by Aradidae, in hind wing venation, male genitalia, spermatheca, claws and eggs, to Pentatomoidea and related groups. However, the female ovipositor was not studied at the time, nor has an attempt been made to homologise its parts on the lines laid down by Snodgrass (1933) for Coreidae and Saldidae: Southwood (1954) has investigated the morphology of the ovipositor in *Aneuris* Curtis and shows that it differs fundamentally from that of *Aradus* Fabricius. Thus one object of the present work has been to examine the ovipositor of *Aradus* in order to establish its homologies and to provide a starting point for work on the higher taxonomy of the so-called Aradoidea.

Tamanini (1950) has claimed that the genital segment of *Aradus* carries two pairs of gonopods; if this is so, then grave doubts must be put upon any grouping of Aradidae with Pentatomomorpha. Investigation of this point is made the second object of this study.

GROUP NOMENCLATURE.

Despite the important nomenclatural work of Van Duzee (1917), confusion still exists as to the names of certain Aradoid groups. Thus numerous works retain the family name Dysodiidae Reuter, but following Van Duzee it is clear that Meziridae should replace this (*Mezira* Amyot and Serville and *Dysodius* Le Pelletier and Serville are undoubtedly members of the same group). It must, however, be pointed out that Aneuridae Douglas and Scott remains available, should it be shown that *Aneuris* Curtis is not a member of the same group as *Mezira*; in current lists *Aneuris* is placed within Meziridae.

Following, for the present, the classification of Reuter as given by Poisson (1951) we have:

Aradoidea.

1. ARADIDAE.

2. MEZIRIDAE.

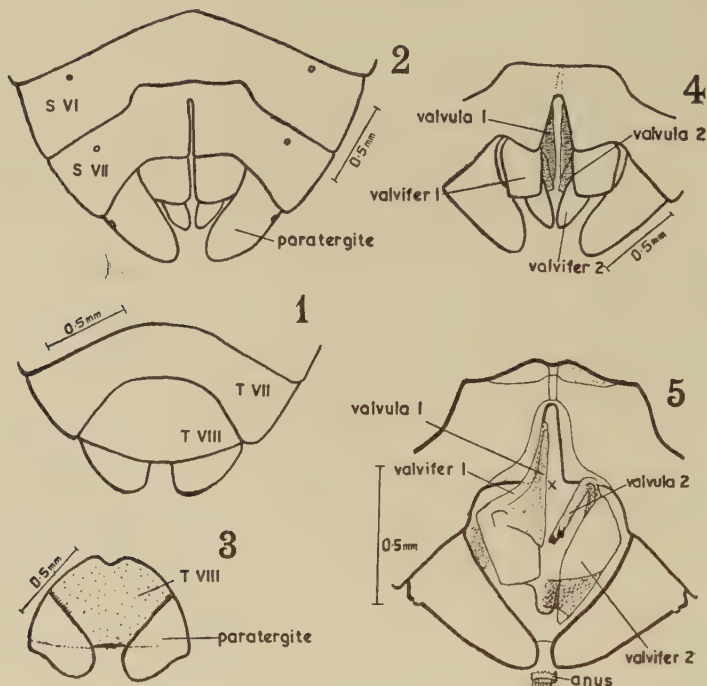
(i) Mezirinae.

(ii) Isoderminae.

3. TERMITAPHIDIDAE.

MATERIAL.

Although a small species and not entirely typical of its genus, *Aradus cinnamomeus* (Panzer) has been used because of its ready availability. The examples used were collected at Oxshott, Surrey, in September, 1953, and probably represented the new generation of the year.



FIGS. 1-5.—*Aradus cinnamomeus* (Panz.), female. (1) Apex of abdomen, dorsal. (2) Apex of abdomen, ventral. (3) Terga VIII, ventral (valvifers removed). (4) Apex of abdomen, ventral (valvifers opened to show valvulae). (5) Ovipositor, viewed from within (right 1st valvifer and left 2nd valvifer removed). x = position of spermathecal duct.

FEMALE GENITALIA.

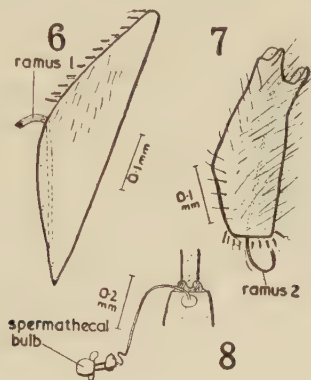
The terminal abdomen, dorsally, is formed by terga VII and VIII: the latter carries a pair of paratergites which are probably merely fragmented parts of the tergum itself. The paratergites fold over and are visible ventrally. Sternum VII is partially split longitudinally along the mid-line; on oviposition the two arms of the split, pseudo-valvifers, open to expose the proximal part of the 1st valvulae. Anteriorly sternum VII is partly covered by the posterior margin of sternum VI.

The 1st valvifers articulate with the paratergites of tergum VIII and carry the 1st valvulae; these are somewhat membranous, ventrally ridged, sparsely pubescent, and with a sclerotic distal apex. The 1st valvulae are closely and broadly attached to the 1st valvifers by the 1st ramus, which is marked by a sclerotic ridge.

The 2nd valvifers are largely concealed, and their articulation with the somewhat membranous terga IX is difficult to observe. Each valvifer carries a single valvula: these latter are sclerotised and rod-like, with a bifid distal apex. Each tip of the bifurcation is densely sclerotic, whilst the 2nd valvula throughout is covered by long, dense and fine pubescence. A sclerotic rod, probably the 2nd ramus, is adherent to the surface of the 2nd valvula and appears to make contact with the 1st ramus.

The genital chamber (vagina, vestibulum) is somewhat sclerotised ventrally and bears a U-shaped projection lying beneath the anus where this passes through the reduced 9th segment: the sclerotisation is an inter-valvifer sclerite and probably of little phylogenetic significance.

The spermatheca leads via a narrow duct into the proximal part of the genital chamber dorsally; anterior to its entry the vagina narrows and there is an M-shaped sclerotisation (perhaps homologous with the ring sclerite of Lygaeidae).



FIGS. 6-8.—*Aradus cinnamomeus* (Panz.), female. (6) 1st valvula. (7) 2nd valvula. (8) Spermatheca and duct.

MALE GENITALIA.

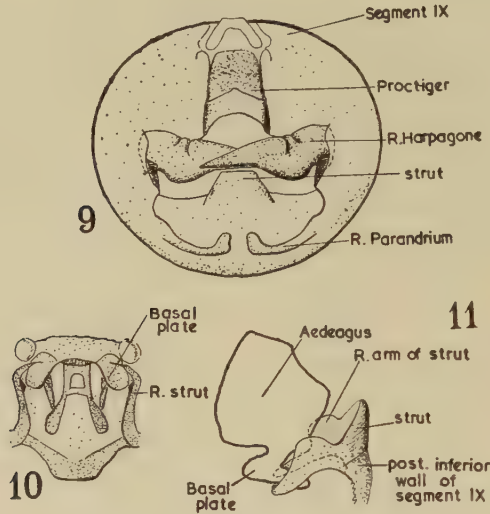
This study is limited to a consideration of the genital segment excluding the aedeagus; the latter has been described by Pruthi (1925). The following account of *A. cinnamomeus* has been found to apply equally to *A. depressus* (Fabricius) with minor, specific, differences.

When viewed apically, the 9th segment is seen to carry a large and symmetrical pair of harpagones (gonopods) lying across the atrium. Below them the posterior wall of the 9th segment is raised on the mid-line, and this raised piece is folded over inwardly: here it bifurcates into two arms and the whole structure forms the aedeagal strut. The two arms of the strut run at right angles to the posterior wall and articulate distally with the large dorsal connective (capitate process) of the basal plate. In *A. cinnamomeus* the dorsal connective is largely sclerotised and its connexion with the strut is an articulation rather than an attachment.

Beneath the harpagones and arising externally from the walls of the genital segment are a pair of processes, hypandria; they are outgrowths of the segmental wall and desclerotised basally.

THE ABDOMEN.

The abdomen in both sexes carries three pairs of dorsal glands. These are usually atrophied in adult Heteroptera, but in *A. cinnamomeus* they persist, opening by a single median pore at the posterior margins of terga III, IV and V.



FIGS. 9-11.—*Aradus cinnamomeus* (Panz.), male. (9) Segment IX, apical. (10) Basal plate from above (aedeagus removed). (11) Aedeagal strut, oblique lateral (aedeagus and basal plate in outline only).

DISCUSSION ON THE FEMALE GENITALIA.

The ovipositor of Saldidae and Coreidae has been studied by Ekblom (1926, 1928) and Snodgrass (1933), of Lygaeidae by Ekblom, and Bonhag and Wick (1953), of Acanthosomatidae by Rosenkranz (1939), and of Pyrrhocoridae by many authors; Weber (1930) and Poisson (1951) give additional data and have evaluated the classical work of Heymons and Berlese. The ovipositor of *Aradus* resembles that of Pentatomidae and Coreidae but the valvulae are separate, sclerotic and distinct whereas in Pentatomidae they are largely fused medially and membranous. The Lygaeid and Pyrrhocorid organ is more of a true lacinate ovipositor, but whether this is a primary or a secondary adaptive character is at present impossible to determine: in its completeness it has affinities with the ovipositor of Saldidae, but in this family the ovipositor is very isolated. The median split of sternum VII is common to many Coreidae and Aradidae but entirely absent in Pentatomidae. Thus, on the evidence of the ovipositor, a structure which has been studied in very few genera as yet, we find Aradidae closely allied to Coreoidea and somewhat less closely to Pentatomoidea. Lygaeidae and Pyrrhocoridae are even further removed, whilst Saldidae are distinctive in having a pair of 3rd valvulae.

DISCUSSION ON THE MALE GENITALIA.

Tamanini (1950) has pointed out that in *Aradus* the 9th male segment carries two sets of processes. He writes "Chiamo questo secondo paio di appendici falsi stili essendo in essi meno evidente l'ufficio di afferratori ed essendo molto più deboli e semplici del primo paio. I falsi stili sono però degli autentici gonopodi del IX sternite, ed in essi è ancora distinguibile una parte prossimale (valva) ed una distale (stilo)." His figures 6 and 12 show the false style demarcated basally from the body of the genital segment, but this is an artifact; the false styles arise at the position Tamanini indicated but they are not at all demarcated from the segment.

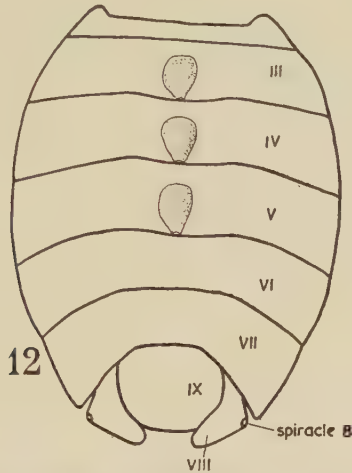


FIG. 12.—*Aradus cinnamomeus* (Panz.), male abdomen from above (semi-diagrammatic).

In *A. cinnamomeus* the "false styles" are basally desclerotised and analogous to the paired outgrowths of *Eurydema* Laporte (Dupuis, 1951) and *Podops* Laporte (Leston, 1953) for which the name parandria has been used. It has been shown (Leston, 1955) in the Pentatomid *Dolycoris baccarum* (Linnaeus) that, in copulation, the harpagones are pressed against the outer surface of the valvifers whilst the expanded conjunctiva presses backwards on the valvifers from within the vagina (cf. Weber, 1930). Although without musculature it is clear that parandria can function in the same manner as the harpagones.

Tamanini's claim to have distinguished a valve and a style is due to the presence of the membranous attachment area ; staining shows no tendon formation, whereas the tendon connecting the base of the harpagones to the basal plate is clearly differentiated, as is the muscle sheet surrounding this base.

The aedeagal strut is a structure of frequent occurrence in Pentatomomorpha and it can be defined as an *inward projection of the postero-inferior wall of the 9th segment, to which is attached the postero-dorsal connectives of the basal plate*. It functions as a means of keeping the aedeagus clear of the posterior wall during erection. In *A. cinnamomeus* the strut is visible externally as a median shelf-like projection of the genital segment.

Tamanini figures the bifid antero-superior projection of the genital segment ; it is present in *A. cinnamomeus* but its homologies are obscure. In *A. cinnamomeus* the proctiger is divided transversely into a sclerotised proximal and a desclerotised distal part, but it would be unwise to consider this as proof of the two-segmented origin of the proctiger (*cf.* Bonhag and Wick, 1953).

ACCESSORY CLASPERS IN PENTATOMOMORPHA.

The widespread occurrence of accessory claspers on the 9th or subsequent segments in male Pentatomomorpha has not previously been pointed out. These structures usually function as extra harpagones but in *Podops* they are, in addition, flaps enclosing the entire atrium. Three forms can be found.

(1) *Parandria*.—Paired outgrowths, fixed or mobile, of the body wall of the 9th segment; without accompanying musculature ; usually desclerotised basally and movable by external pressure (i.e., from an expanding aedeagus or from the female valvifers). Found in *Aradus*, *Podops*, all genera of Discocephalini, *Eurydema*.

(2) *Atrial sclerotisations*.—Paired sclerotisations of the membranous floor of the genital atrium. Found in all Amyoteinae (= Asopinae), where they sometimes surpass the harpagones in size ; many genera of Pentatominae.

(3) *Proctigeal appendages*.—Paired outgrowths of the proctiger laterally, movable by virtue of a basal desclerotisation. Found in *Pachycoris* Burmeister and some other genera of Tetyrini (= Pachycorini).

CONCLUSIONS.

1. The ovipositor of *Aradus* is of the same general form as in Pentatomoidea and Coreoidea, but more closely allied to the latter.

2. The male genital segment contains no features sharply differentiating it from that of Pentatomoidea, Coreoidea and Lygaeoidea.

3. The so-called 2nd gonopods are parandria, paired outgrowths of the segmental wall without musculature.

4. In *A. cinnamomeus* the dorsal abdominal glands persist in the imagines of both sexes.

ACKNOWLEDGMENTS.

Mr. T. R. E. Southwood has discussed the subject matter of this paper with the author and has allowed the use of unpublished data ; Mr. R. E. Snodgrass kindly supplied a copy of his important paper (1933) ; certain concepts were discussed freely with Dr. J. G. Pendergrast : all three gentlemen are thanked for their assistance.

SUMMARY.

The male and female genitalia of *Aradus cinnamomeus* (Panzer) have been studied. The female ovipositor has been homologised on the lines laid down by Snodgrass and is shown to differ but little from the ovipositor of Coreoidea and Pentatomoidea, and is closely allied to the ovipositor of the former. The male genital segment is constructed upon the same lines as that of all Pentatomomorpha ; the so-called 2nd gonopods are shown to be parandria, i.e., outgrowths of the segmental wall without musculature but movable by virtue of their mem-

branous base when external pressure is applied. A classification of accessory claspers of the 9th and subsequent segments is put forward. In both sexes the dorsal abdominal glands persist in imagines.

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SEX RATIOS AMONG BRITISH *CULICOIDES*.

By D. S. KETTLE, D.Sc.(Lond.), F.R.E.S.

EARLY in 1945 entomologists from the four Scottish Universities began to study the abundance and variety of *Culicoides* throughout Scotland. In their report (Cameron *et al.* 1946) attention was drawn to the abnormal sex ratios encountered in *C. impunctatus* and *C. obsoletus*, in which only a very small percentage (< 5 per cent.) of males were found although various, but unspecified, methods of collecting were employed. At the same time, the sex ratios of *C. pulicaris* and *C. grisescens* were found to be more normal. Parker (1949), using a standard sweep net technique, found highly significant deviations from a 1:1 sex ratio in all the species he collected (Table I). His work provided a possible explanation of the earlier results because he showed that, in *C. pallidicornis* at least, the time of activity of the sexes was markedly different. The females did not appear until the peak of male activity was passed.

TABLE I.—*Summary of published data on sex ratios in various British species of Culicoides. *; **; *** indicate where the Chi-square test exceeds the 0.05, 0.01 and 0.001 levels of significance.*

Species.	Males.	Females.	Total.	Females (per cent.).	Author.	Sampling method.
<i>albicans</i> .	86	118	204	58 *	Cameron (1948)	Box traps
<i>delta</i> .	43	17	60	28 ***	Cameron (1948)	" "
<i>grisescens</i> .	.	.	.	c60	Cameron <i>et al.</i> (1946)	Various
<i>heliophilus</i> .	55	62	117	53	Cameron (1947)	Box traps
" .	31	30	61	49	Cameron (1948)	" "
" .	3	63	66	95 ***	Parker (1949)	Sweep net
<i>impunctatus</i> .	.	.	.	96-99	Cameron <i>et al.</i> (1946)	Various
" .	0	20	20	100 ***	Cameron (1947)	Box trap
" .	48	54	102	53	Cameron (1948)	" "
" .	15	220	235	94 ***	Parker (1949)	Sweep net
" .	36,831	25,643	62,474	41 ***	Kettle (1951)	Sticky traps
<i>obsoletus</i> .	.	.	.	c99	Cameron <i>et al.</i> (1946)	Various
" .	11	9	20	45	Hill (1947)	Rearing larvae
" .	30	119	149	80 ***	Cameron (1947)	Box traps
" .	81	24	105	23 ***	Cameron (1948)	" "
" .	12	90	102	88 ***	Parker (1949)	Sweep net
<i>pallidicornis</i> .	62	79	141	56	Cameron (1947)	Box traps
" .	415	478	893	54 *	Cameron (1948)	" "
" .	1,075	529	1,604	33 ***	Parker (1949)	Sweep net
<i>pulicaris</i> .	.	.	.	c50	Cameron <i>et al.</i> (1946)	Various
" .	28	42	70	60	Cameron (1947)	Box traps
" .	46	101	147	69 ***	Cameron (1948)	" "
" .	113	18	131	14 ***	Parker (1949)	Sweep net
<i>truncorum</i> .	28	32	60	53	Cameron (1948)	Box traps

Cameron (1947 and 1948) used box traps to identify the breeding sites of various *Culicoides*. The newly emerged adults were attracted by daylight to

enter glass tubes fitted with a cone trap. Such a technique almost amounts to a field method of rearing adult *Culicoides* and one would expect it to yield unbiased data. For some unaccountable reason the results obtained by this method were inconsistent (Table I). Thus one year (Cameron 1947) there was a highly significant excess of female over male *C. obsoletus*, and in the following year the position was reversed (Cameron 1948).

TABLE II.—*Sex ratio in various species of Culicoides obtained by rearing larvae 1948–1954. * and ** indicate where the Chi-square test exceeds the 0.05 and 0.01 levels of significance respectively.*

Species.	Males.	Females.	Total.	Females (per cent.).
<i>albicans</i>	18	4	22	18 **
<i>chiopterus</i>	20	38	58	66 *
<i>circumscriptus</i>	10	17	27	63
<i>circumscriptus</i> ?	18	11	29	38
<i>cubitalis</i>	51	70	121	58
<i>cunctans</i>	8	5	13	38
<i>duddingstoni</i>	15	12	27	44
<i>fascipennis</i>	15	18	33	55
<i>halophilus</i>	5	9	14	64
<i>heliophilus</i>	22	20	42	48
<i>impunctatus</i>	40	41	81	51
<i>lupicaris</i>	5	7	12	58
<i>maritimus</i>	12	9	21	43
<i>nubeculosus</i>	7	7	14	50
<i>obsoletus</i>	24	29	53	55
<i>odibilis</i>	50	55	105	52
<i>pallidicornis</i>	34	47	81	58
<i>pulicaris</i>	64	88	152	58
<i>punctatus</i>	8	4	12	33
<i>riethi</i>	17	17	34	50
<i>salinarius</i>	43	23	66	35 *
<i>scoticus</i>	7	3	10	30
<i>stigma</i>	14	11	25	44
<i>truncorum</i>	26	40	66	61
<i>vexans</i>	16	15	31	48
type XXIV n. sp. . . .	6	4	10	40
<i>circumscriptus</i> or <i>salinarius</i>	2	2	4	24 58
<i>delta</i>	1	7	8	
<i>grisescens</i>	4	2	6	
<i>pictipennis</i>	2	3	5	
<i>simulator</i>	1	0	1	
TOTAL	565	618	1183	52.2

During the past six years numerous adult *Culicoides* have been reared from larvae in order to relate these two stages in the life cycle. The data so obtained are summarised in Table II, and it will be noticed that significant deviations from a normal sex ratio are rare, the 5 per cent. level of significance being exceeded only three times in twenty-seven Chi-Square tests, whereas one would expect to exceed this level 1.35 times in the same number of observations on a normally sexed population. Hence it is unwise to attach any importance to the deviations from normality found in *C. chiopterus* and *C.*

salinarius, which can be regarded as due to random error. While it is possible that the abnormal sex ratio recorded in Table II for *C. albicans* might be real, it is not considered likely in view of the overwhelming evidence presented in the rest of the table for normal sex ratios in *Culicoides*.

Larval rearing has also been done by Hill (1947) who obtained a normal sex ratio in *C. obsoletus* (Table I).

It follows therefore that any unusual sex ratio encountered in field studies, as for example the excess of male *C. impunctatus* on sticky traps (Kettle 1951; Table I) requires some other explanation, such as differential activity or mortality.

SUMMARY.

1. More consistent results were obtained on the sex ratios of *Culicoides* by rearing mature larvae than by sweep net, sticky trap or box trap collections.
2. Among twenty-six species of British *Culicoides* the sex ratio is normal.

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THE MORPHOLOGY OF THE HEAD OF THE
FINAL INSTAR LARVA OF *NASONIA VITRIPENNIS* WALKER
(HYMENOPTERA : CHALCIDOIDEA).

By J. R. CUTLER, B.Sc.

(*Natural History Department, University of Aberdeen.*)

(*Communicated by J. R. T. SHORT, Ph.D., F.R.E.S.*)

1. INTRODUCTION.

THE aim of this study has been to give an accurate description of the external features together with the distribution of the muscles and the internal skeletal structures of the head of a final instar larva of *Nasonia vitripennis* Walker. An attempt has been made to homologise the head structures with those of the heads of generalised pterygote insects, e.g. Orthoptera, and to compare the Chalcidoid head with that of the Ichneumonoids at the same stage of development.

2. ACKNOWLEDGMENTS.

I am greatly indebted to Dr. J. R. T. Short, under whose supervision this work was carried out.

I am grateful to Dr. S. Symmons who assisted me in methods of fixing and sectioning the material.

The larvae of *N. vitripennis* were provided through the kindness of Dr. R. L. Edwards, of University College, Hull.

3. MATERIAL AND TECHNIQUE.

The larvae were sent from Hull within the puparia of the host *Musca domestica* L. The larvae were cut open at the posterior end and then quickly dropped into alcoholic Bouin's Fixative, which was hot to ensure rapid and thorough fixation. In order to minimise the hardening effect of hot wax on the cuticle, the larvae were impregnated in a vacuum oven for two hours and then embedded in 62° C. m.p. wax. Three series of transverse and longitudinal sections were cut at a thickness of 7 μ . Mallory's Triple Stain was used according to the method outlined by Pantin (1946). The sections were mounted in euparal. They were reproduced on paper using camera lucida and these figures used in the reconstruction of the head according to Pantin (1946 : 50, Method 1).

Fresh unmounted larvae were studied to reveal the positions of grooves, and larvae mounted in gum chloral to indicate spines and ridges. To study the tentorium, several heads were cleared in 10 per cent. KOH, stained and mounted. Whole heads were also soaked in a weak solution of iron alum and then treated with freshly prepared pyrogallous acid solution. This stains the muscles deep black.

4. TERMINOLOGY AND NOMENCLATURE.

To avoid confusion when homologising, the terminologies of Snodgrass (1928, 1935, 1947) and Short (1951, 1952) are used and the numbers given to the muscles in the Orthopteroid head by Snodgrass (1928) have been used for their suggested homologues in the head of *N. vitripennis*. The generic name *Nasonia* now takes precedence over *Mormoniella*—see Hemming (1953).

5. PREVIOUS MORPHOLOGICAL WORK ON CHALCIDOIDS.

Most of the work done on Chalcidoids has been concerned with the biology and economic importance of these parasites. Tiegs (1922) gave a brief description of external features in a paper on metamorphosis. Parker (1924) made a wide study of the externals of Chalcidoids but did not mention the internal morphology of the head. Salt (1931), Evans (1933) and a number of other workers have published papers on the parasites, Ichneumonoid and Chalcidoid, of various crop pests, briefly describing the external head structures. The most recent description of externals is given by Short (1952). No paper has been found which describes the internal morphology of the head of Chalcidoids.

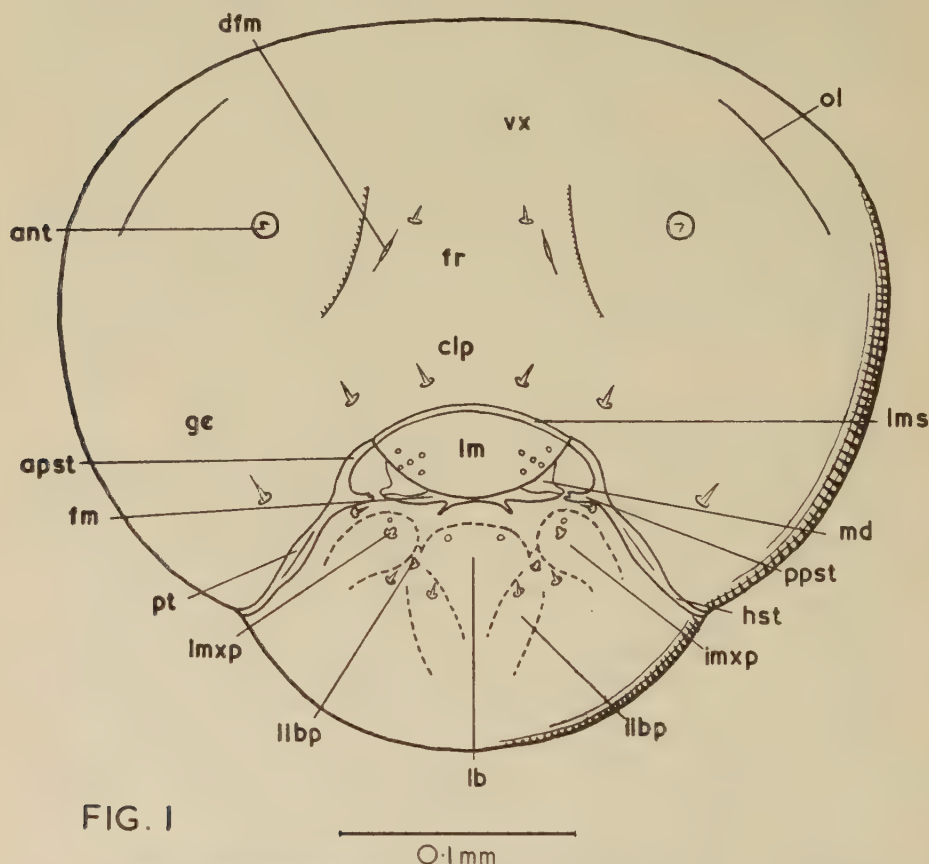


FIG. 1

FIG. 1.—Head of *Nasonia vitripennis*. Anterior view. See Section 7 for abbreviations.

6. (a) GENERAL COMMENTS ON THE HEAD.

As a result of the parasitic mode of life, the head is highly specialised and shows a number of reductions. It appears from Parker's work (1924) that the main features of the Chalcidoid head are fairly constant but that minor differences in the shape of the mandibles and distribution of the sensilla occur.

(b) *Cranium*.

The word cranium in this account is equivalent to the epicranium of Vance and Smith (1933).

Slightly ventral of a hypothetical line drawn between the antennae (fig. 1; *ant.*) are the grooves (*dfm*) made by the attachment to the frons (*fr*) of the precerebral pharyngeal (fig. 2; 35, 36, 39) and dorsal hypopharyngeal (38) muscles. These grooves were thought by Snodgrass (1947) to be the remnants of the frontal cleavage lines and by Vance and Smith to be the pits of the dorsal tentorial arms. Glover (1934) noticed that the cleavage lines are not present in the mature larvae of Braconids and Short (1952) showed that when cleavage occurs it takes place along a dorsal median line from the postoccipt (fig. 2, *poc*) through the frons to the clypeal region (*clp*). He also discovered that the dorsal tentorial marks are situated elsewhere.

The frons (*fr*) and clypeus (*clp*) are not differentiated by an epistomal ridge. The dorsal limit of the clypeus may be determined by the position of the attachment of the clypeal dilators (fig. 2; 33, 34) of the pharynx and cibarium (*cb*). The lower limit is defined by a ridge which Parker called the "facial arc," Cameron (1938) the "clypeal arch" and Vance and Smith and Short the "labral sclerite" (*lms*).

The ocular line of Short (1952) is situated dorso-lateral to each antenna. It defines the position of the developing imaginal eye. The ocular line is called the temporal suture by Vance and Smith.

(c) *Tentorium*.

The tentorium is highly specialised. The posterior tentorial pits (fig. 1, *pt*) which are long and narrow, are situated on the hypostoma (*hst*) posterior to the mandibles (*md*). From the pits, two stout arms proceed backwards and slightly inclined towards the mid-line to a point just anterior to the first thoracic segment. Here a transverse bar (figs. 2, 4, *tb*) unites the two arms, thus forming a U-shaped structure. This is the complete tentorium. In his figure of the head of *Stenomalus liparæ* (Giraud) Short indicates the presence of anterior tentorial pits. These were not found in *N. vitripennis*.

(d) *Stomodaeal muscles*.

The dorsal dilators of the stomodaeum are divided into two groups by the interposition of the frontal ganglion (fig. 2, *fg*). Anterior to the ganglion there are four pairs of cibarial dilator muscles (33, 34) which take their origin on the clypeus. There are no labral retractors or compressors. Posterior to the frontal ganglion and encircled by its commissures (*fge*) is the second group of dorsal pharyngeal dilators (35, 36, 39). The most posterior pair (39) have their origin slightly mesad of the origin of the dorsal hypopharyngeal muscles (38). Dorsal dilators of the postpharynx are absent.

The anterior ventral stomodaeal dilator (41) takes its origin from the tentorial bar and is inserted on the suspensorial sclerite of the hypopharynx (*sh*). Posterior to this muscle are the ventral dilators of the pharynx (43) and post-pharynx (44) which also take their origin from the tentorial bar (*tb*).

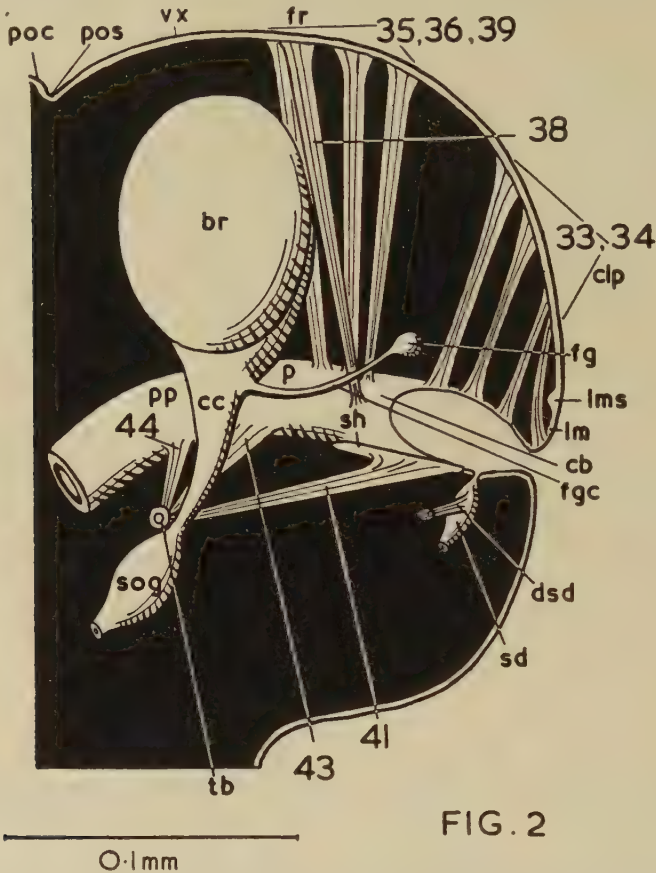


FIG. 2.—Lateral view of the head drawn as a dissected object, showing stomodaeal muscles.
See Section 7 for abbreviations.

(e) *Hypopharynx and Salivary Duct.*

The hypopharynx is fused to the labium and maxillae, which grow forward so as completely to enclose it within the mouth cavity. The suspensorial sclerite (*sh*) occurs as a thickening and hardening of the cuticle to which are attached the dorsal hypopharyngeal (38) and ventral stomodaeal dilator (41) muscles. The paired salivary ducts join to produce a single duct (*sd*) which opens at the anterior end of the hypopharynx (fig. 2). The salivary duct orifice is controlled by a single pair of muscles (*dsd*) which have a lateral insertion on the duct and which take their origin from the same points on the tentorium as the maxillary and labial muscles (fig. 4; 12, 13, 14, 23, 24).

(f) *Appendages.*(i) *Antennae* (fig. 1, *ant.*)

Each antenna is in the form of a small conical tubercle which arises from a circular membranous socket. There are no antennal muscles.

(ii) *Mandibles and Muscles* (fig. 3).

The mandibles are heavily sclerotised and dark brown in colour. They are roughly triangular, being sharply pointed at the free end but bearing no smaller accessory teeth. The anterior pleurostomal process (fig. 1, *apst*) is rounded and articulates with a slight depression in the mandible. The posterior process (fig. 1, *ppst*) presents a socket for the mandibular condyle.

The abductors (8) and adductors (9) of the mandibles have been drawn separately in fig. 3 in order to avoid overlapping. The abductors take their origin anterior to the adductors on the cranial wall.



FIG. 3

0.1mm

FIG. 3.—Anterior view of the head drawn as a dissected object showing mandibular articulations and muscle insertions. See Section 7 for abbreviations.

(iii) *Maxillae and Muscles* (figs. 1 and 4).

The area ventral to the mouth is membranous, showing no differentiation into maxillary and labial sclerites. However, a pair of maxillary palps in the form of minute tubercles (*lmaxp*) are present. In a cleared specimen, the developing imaginal maxilla and maxillary palp (fig. 1, *imaxp*) are visible and give an indication of the extent of the larval structures.

A single muscle (fig. 4; 12, 13, 14) is inserted near the tip of each maxilla. It takes its origin on the tentorial arm of each side just before the arms are joined by the transverse tentorial bar (*tb*).

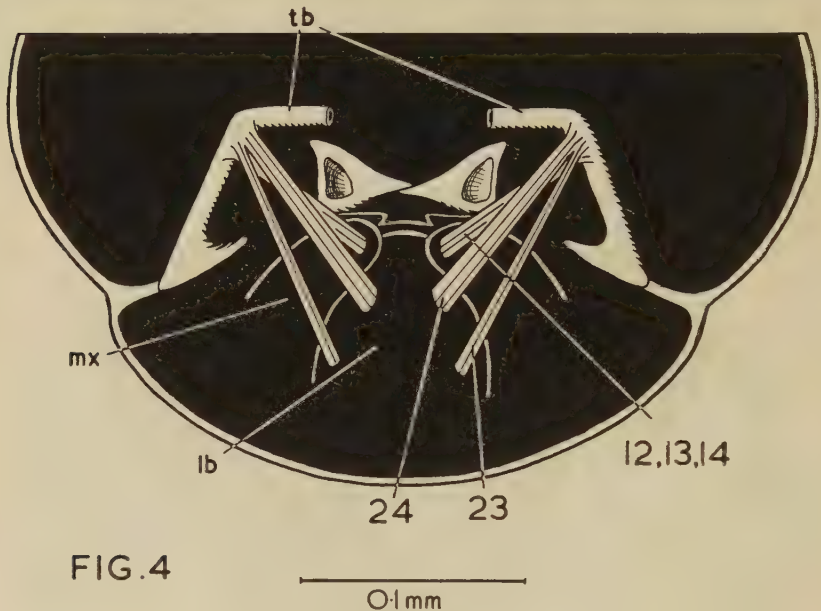


FIG. 4

0.1 mm

FIG. 4.—Posterior view of the head drawn as a dissected object showing the maxillary and labial muscles with their origin on the tentorium. See Section 7 for abbreviations.

(iv) *Labium and Muscles* (figs. 1 and 4).

The labium, like the maxillae, shows no differentiation but possesses a pair of minute labial palps (fig. 1, *lbp*). No groove or sulcus separating the prementum from the postmentum was found.

Two pairs of muscles (23, 24) corresponding to the retractors of the prementum are inserted on the labium. Since no muscles insert on the postmentum of Orthopteroids, the postmentum of *N. vitripennis* may be held to commence immediately posterior to the posterior retractor muscle (23). Both pairs of muscles take their origin on the tentorium at the points where the transverse bar joins the arms (fig. 4).

(g) *Food meatus* (fig. 1, *fm*).

In Orthopteroids the hypopharynx lies free within the preoral cavity, giving rise to a ventral salivary meatus and a dorsal food meatus. In *N. vitripennis* the hypopharynx is fused with the cibarium and the salivary meatus is absent. Hence it has been thought more accurate to describe the preoral cavity of *N. vitripennis* as the food meatus.

(h) *Setae and Sensilla*.

Two types of sensory structures are present on the head. The spines or setae are comparatively large on the cranial region. A single pair occurs between the antennae and three pairs are distributed in an arc dorsal to the labral sclerite (*lms*) and hypostoma (*hst*). Ventral to the mouth there are three pairs of setae. Five pairs of minute sensilla are located on the labrum (*lm*) and two pairs on the underlip complex.

7. SUMMARY OF INTERPRETATIONS.

List of Head Muscles.

- | | |
|--|---|
| 8, abductor of mandible. | 35, 36, 39, anterior dilators of pharynx or precerebral pharyngeal muscles. |
| 9, adductor of mandible. | 38, dorsal hypopharyngeal muscle. |
| 12, proximal adductor of stipes. | 41, ventral dilator of cibarium and buccal cavity. |
| 13, anterior adductor of stipes. | 43, ventral dilator of pharynx. |
| 14, cranial flexor of lacinia. | 44, ventral dilator of postpharynx. |
| 23, posterior retractor of prementum. | <i>dsd</i> , dilators of salivary duct. |
| 24, anterior retractor of prementum. | |
| 33, 34, anterior dilators of cibarium and buccal cavity. | |

List of Abbreviations Used in Figures.

- | | |
|---|---|
| <i>ant</i> , antenna. | <i>lmaxp</i> , larval maxillary palp. |
| <i>apst</i> , anterior pleurostomal process. | <i>lm</i> , labrum. |
| <i>br</i> , brain. | <i>lms</i> , labral sclerite. |
| <i>cb</i> , cibarium. | <i>md</i> , mandible. |
| <i>cc</i> , circumoesophageal connectives. | <i>mx</i> , maxilla. |
| <i>clp</i> , clypeus. | <i>ol</i> , ocular line. |
| <i>dfm</i> , depressions of cranial wall at origins of frontal muscles. | <i>p</i> , pharynx. |
| <i>fg</i> , frontal ganglion. | <i>poc</i> , postocciput. |
| <i>fgc</i> , frontal ganglion connectives. | <i>pos</i> , postoccipital sulcus. |
| <i>fm</i> , food meatus. | <i>pp</i> , postpharynx. |
| <i>fr</i> , frons. | <i>ppst</i> , posterior pleurostomal process. |
| <i>ge</i> , gena. | <i>pt</i> , posterior tentorial pit. |
| <i>hst</i> , hypostoma. | <i>sd</i> , salivary duct. |
| <i>ilbp</i> , labial palp of imago. | <i>sh</i> , suspensorium of hypopharynx. |
| <i>imaxp</i> , maxillary palp of imago. | <i>sog</i> , suboesophageal ganglion. |
| <i>lb</i> , labium. | <i>tb</i> , tentorial bar. |
| <i>lbp</i> , larval labial palp. | <i>vx</i> , vertex. |

8. DISCUSSION AND COMPARISON OF THE CHALCIDOID HEAD AS SEEN IN *N. vitripennis* WITH THAT OF ICHNEUMONIDS.

A number of modifications of the head result from the larval habits of Chalcidoids. Cocoons are seldom formed. Coupled with this is the loss of the silk press, characteristic of Ichneumonoids, and a reduction in the extent of sclerotisation. Except for the labral sclerite, pleurostoma and hypostoma, the head is only slightly sclerotised and possesses none of the strengthening sclerites, e.g., sclerotic spur of hypostoma, stipital and labial sclerites, found in the Ichneumonoid head.

A feature of *N. vitripennis* and probably of most other Chalcidoids is the tendency towards a prognathous condition which results from the forward growth of the underlip complex.

The head musculature is similar to that of Ichneumonoids, except that the salivary duct muscles take their origin on the tentorium, not on the hypopharyngeal and labial sclerites. The labrum, which is membranous, has no labral compressors or retractors attached to it and the dorsal dilators of the postpharynx are also absent. Because of their position and function the four pairs of clypeal muscles have been homologised to numbers 33 and 34 of Snodgrass. Similarly the maxillary muscle would appear from its insertion and origin to combine the functions of the adductors of the stipes (12, 13) and the cranial flexor of the lacinia (14).

The most notable departure from the Ichneumonoid type of head is in the structure of the tentorium. It appears to be formed from the posterior arms and tentorial bar alone. The posterior pits are situated on the anterior surface of the head, not on the lateral surface as in Ichneumonoids. This migration may be caused by the tendency towards prognathism. There are no anterior and dorsal arms nor are there any signs of the anterior pits. The tentorium is strongly sclerotised since it gives attachment to a large number of muscles.

9. SUMMARY.

1. Methods and technique of studying the material and a review of previous literature are given.

2. The head shows certain specialisations, e.g. the light sclerotisation of the cranium and the completely membranous nature of the underlip complex. Also the prognathous condition carries the posterior tentorial pits on to the anterior surface of the head. The tentorium is reduced and consists of the posterior arms and transverse bar alone.

3. The absence of the labral compressors and retractors and also the dorsal postpharyngeal dilators was noted. The salivary duct muscles take origin from the tentorium.

4. A brief comparison of the Chalcidoid and Ichneumonoid head is made.

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A NOTE ON INTRA-SPECIFIC VARIATION OF CHAETOTAXY IN A LEPIDOPTEROUS LARVA.

By J. R. WILLIAMS, B.Sc., D.I.C., F.R.E.S.

INTRODUCTION.

IN an earlier paper (Williams, 1953) I described several lepidopterous larvae of agricultural importance, one of which was *Cryptophlebia williamsi* Brad. (Eucosmidae), a very common pest of *Cajanus cajan* and *Canavalia ensiformis* in Mauritius. At a later date, when examining a few larvae of that species, the subventral setal group on the ninth abdominal segment was found to be bisetose, whereas in the published description it had been given as unisetose and as such employed as a key character.

Reference to the mounted larval skin upon which the description of the chaetotaxy was based showed the setal group in question to be unisetose as was described. The preserved complete specimens which had been used in conjunction with the mounted skin when forming the description were then referred to; these were fifteen in number and the following surprising variation of the subventral group on the ninth abdominal segment was found:

Unisetose	4 larvae
Bisetose	7 „
Unisetose on right, bisetose on left	2 „
Unisetose on left, bisetose on right	1 larva
Bisetose on left, trisetose on right	1 „

The same larvae were then scrutinised for other variable chaetotaxic characters which might also have led to descriptive errors. None was found, however, and further observations were then made upon the reliability of the setal characters by collection and examination of a large number of larvae, particular attention being given to the subventral setae on the ninth abdominal segment. These observations are described below. The nomenclature used for the setae is that proposed by Hinton (1946).

VARIATIONS OF SETAL PATTERN ON LARVAE OF *CRYPTOPHLEBIA WILLIAMSII*

In February, 1953, 144 fully grown, or nearly fully grown, larvae were collected from *Cajanus cajan*, and in April of the same year another 550 were collected from a plot of *Canavalia ensiformis* about five miles distant. One hundred larvae were taken randomly from each collection and all groups of the tactile setae (or long setae, *vide* Hinton, 1946) on abdominal segments 1-9 inclusive were examined under a binocular microscope. Setae missing from natural causes, as shown by the absence of both seta and socket (and as opposed to setae broken off by accident), were recorded. The results are given in Tables A and B. The remaining larvae were examined only for the subventral (SV) group of setae on the ninth abdominal segment.

PROC. R. ENT. SOC. LOND. (A) 30. PTS. 4-6. (JUNE, 1955).

TABLE A.—*Larvae from Cajanus cajan. Number and location of missing tactile setae on abdominal segments 1-9 of 100 larvae.*

Abdominal segment.	Side of body.	Seta :											Total setae missing.
		D1.	D2.	SD1.	SD2.	L1.	L2.	L3.	SV1.	SV2.	SV3.	V1.	
1	{L	1	.	1	1	1	3	3	1	.	4	.	15 9}
	{R	.	.	.	.	1	.	.	.	3	5	.	
2	{L	1	1	2	2	1	4	1	.	.	1	.	13 5}
	{R	.	.	.	.	.	2	3	.	.	.	.	
3	{L	2	3	1	.	2	5	2	1	1	1	.	18 10}
	{R	1	.	.	.	2	2	2	.	1	2	.	
4	{L	.	3	.	.	4	3	2	.	.	.	.	12 13}
	{R	2	3	2	1	3	.	2	.	.	.	.	
5	{L	1	2	1	.	1	1	.	.	1	1	.	8 6}
	{R	3	2	.	.	1	.	.	.	.	.	.	
6	{L	1	1	.	.	1	3	3	.	1	1	.	11 4}
	{R	2	1	.	.	.	1	.	.	.	.	.	
7	{L	1	.	1	.	.	2	.	1	4	6	.	15 9}
	{R	.	.	.	.	1	1	1	1	1	4	.	
8	{L	2	.	1	.	.	2	6	1	1	*	1	14 11}
	{R	2	2	1	1	.	.	4	.	.	*	1	
9	{L	.	1	1	.	1	1	4	.	23	*	1	32 40}
	{R	.	2	.	.	3	1	6	1	26	*	1	
Total setae missing	{L	9	11	8	3	11	24	21	4	31	14	2	138
	{R	10	10	3	2	11	7	18	2	31	11	2	107
	{L+R	19	21	11	5	22	31	39	6	62	25	4	245

* Seta SV3 does not occur on Segments 8 and 9.

Eighty larvae did not have the full complement of setae.

Setal pairs (the same seta on both sides of the body) were missing with the following frequency :

Setae	D1 on segment 6	.	.	1 larva
„ D1 „ „	8	.	.	1 „
„ D2 „ „	3	.	.	1 „
„ D2 „ „	6	.	.	1 „
„ D2 „ „	9	.	.	1 „
„ L3 „ „	8	.	.	1 „
„ SV3 „ „	7	.	.	1 „
„ SV2 „ „	9	.	.	9 larvae

The data given in Tables A and B may be elaborated as follows:—

1. Setae were missing more frequently with larvae from *Cajanus* than with those from *Canavalia*. 80 per cent. of the former and 55 per cent. of the latter did not have the full complement of tactile setae on abdominal segments 1-9, while the total numbers of these setae missing from the 100 larvae of each collection were 245 and 95 respectively. It is concluded that the degree of chaetotaxic inconsistency may vary appreciably among larvae collected under different circumstances.

TABLE B.—*Larvae from Canavalia ensiformis. Number and location of missing tactile setae on abdominal segments 1-9 of 100 larvae.*

Abdominal segment.	Side of body.	Seta											Total setae missing.
		D1.	D2.	SD1.	SD2.	L1.	L2.	L3.	SV1.	SV2.	SV3.	V1.	
1	{L	.	.	.	.	1	1	.	.	1	4	.	13
	{R	.	.	.	.	.	2	.	.	1	3	.	
2	{L	1	1	.	.	.	1	.	.	.	1	.	7
	{R	2	.	.	.	1	.	.	.	.	.	.	
3	{L	1	2	.	.	.	.	.	1	.	.	.	4
	{R	.	.	.	.	.	.	.	.	.	.	.	
4	{L	.	.	1	1	1	1	.	.	.	.	.	6
	{R	.	.	.	.	.	.	1	.	1	.	.	
5	{L	.	.	2	.	.	.	.	.	.	.	.	4
	{R	1	1	.	.	.	.	.	.	.	.	.	
6	{L	1	2	.	.	.	1	.	.	.	.	.	5
	{R	1	.	.	.	.	.	.	.	.	.	.	
7	{L	1	1	1	1	.	.	.	.	.	5	.	15
	{R	2	1	1	.	.	2	.	.	.	.	.	
8	{L	.	.	1	1	1	.	1	.	.	*	.	4
	{R	.	.	.	.	.	.	.	.	.	*	.	
9	{L	.	1	.	.	.	.	5	.	14	*	1	37
	{R	.	.	.	.	.	1	5	.	10	*	.	
Total setae missing	{L	4	7	5	3	3	4	6	1	15	10	1	95
	{R	6	2	1	0	1	5	5	1	11	4	0	
	{L+R	10	9	6	3	4	9	11	2	26	14	1	

* Seta SV3 does not occur on Segments 8 and 9.

Fifty-five larvae did not have the full complement of setae.

Setal pairs (the same seta on both sides of the body) were missing with the following frequency :

Setae D1	on segment 7	.	.	1 larva
„ D2	„ „	7	.	1 „
„ L3	„ „	9	.	1 „
„ SV2	„ „	9	.	4 larvae

2. The actual number of missing setae was insignificant when expressed as a percentage of the full complement. The full complement of tactile setae on abdominal segments 1-9 of *C. williamsi* is 194, and the average number of such setae missing from 100 larvae when expressed as a percentage of the full complement is 1.26 and 0.49 for larvae from *Cajanus* and *Canavalia* respectively. If the average number of missing setae is calculated only from those larvae without a full complement, the figures become 1.58 and 0.89 respectively. In other words, while the chaetotaxic variation was appreciably different in the two collections, it was very small in both,

3. Seta SV2 on 9 was missing with greater frequency than other setae. Otherwise, the distribution of missing setae was haphazard, showing no discernible pattern, although there was some indication of setae SD2, SV1, and V1 being less frequently absent than other setae.

4. The lack of discernible pattern in the distribution of missing setae (apart from the pronounced liability for SV2 on 9 to be missing) may be gauged by comparing the total number of setae which were absent and the number of setal pairs which were absent. Thus, with the 100 larvae from *Cajanus*, there was a total of 245 missing setae, but among these were only 16 pairs of setae, nine of which were pairs of SV2 on 9. A similar comparison may be made with the 100 larvae from *Canavalia*. Furthermore, apart from SV2 on 9, no setal pair was absent on more than one occasion from the total of 200 larvae, e.g., D1 was absent on both sides of segment 6 with only one larva out of the 200, similarly with L3 on both sides of 9, etc. The probability of the pair D1 on 6, or L3 on 9, being absent from larvae of *C. williamsi* is therefore in the order of 1 in 200, and the same applies to all other setal pairs which were missing, apart from the pair SV2 on 9.

As already stated, the SV groups of setae on segment 9 were examined on all the larvae collected. The results were as follows:

Condition of the SV setal group on abdominal segment 9.

(a) 144 larvae from *Cajanus* :

	Number of larvae.	Frequency	
Bisetose	90	7.5	1.7
Unisetose	12	1.0	
Unisetose on left, bisetose on right	19	3.5	1.0
Bisetose on left, unisetose on right	21		
Trisetose on left, bisetose on right	1		
Bisetose on left, nil on right	1		

(b) 550 larvae from *Canavalia* :

	Number of larvae.	Frequency	
Bisetose	404	16.2	2.8
Unisetose	25	1.0	
Unisetose on left, bisetose on right	59	4.8	1.0
Bisetose on left, unisetose on right	50		
Trisetose on left, bisetose on right	5		
Bisetose on left, trisetose on right	4		
Trisetose on left, unisetose on right	1		
Trisetose	1		
Bisetose on left, nil on right	1		

The figures show that the SV group on abdominal segment 9 is normally bisetose, although its composition is variable owing to the absence from one side or the other, or from both sides, of SV2. Occasionally, however, an additional seta is present so that the group is trisetose, while very occasionally the group is entirely absent. The important point which emerges from the data is that the composition of the SV setal group on abdominal segment 9 is too variable

for its use as a character to aid identification. Its bisetose nature is a statistical character of the species, and therefore of little value as a recognition character.

CONCLUSIONS.

The chaetotaxy of lepidopterous larvae provides a large number of distinct characters on these relatively unspecialised and morphologically simple bodies. The characters it provides are also of good taxonomic standing, for the setae of different species are clearly homologous. If descriptions of lepidopterous larvae are to be adequate it is therefore desirable that careful treatment be accorded to their chaetotaxy.

An aspect of larval chaetotaxy which does not seem to have previously received critical attention is the degree of individual variation and the relative stability of the composition of the various setal groups. A general appreciation of the likely extent and nature of chaetotaxal variation among lepidopterous larvae may be possible if several species belonging to different groups are studied in this respect. Such an appreciation would, of course, be valuable when forming descriptions, and would tend to avoid errors such as that which led to the present study.

Two facts emerge from this inquiry into the setal variations among larvae of *Cryptophlebia williamsi*. Firstly, many larvae do not have the full complement of setae, but the individual aberrations are small and do not compromise the recognition of a definite setal pattern for the species. Secondly, on one segment (abdominal segment 9) one setal group (the SV group) varies in its composition to an extent which is appreciably greater than that shown by other groups, and frequently enough to preclude its employment as a specific character in the absence of a series of specimens.

SUMMARY.

The variability of the setal characters on larvae of the Eucosmid *Cryptophlebia williamsi* Brad. was assessed by examining the tactile setae on abdominal segments 1-9 of two hundred larvae.

It was found that the variations of setal pattern were small and unimportant, except that on segment 9 the composition of the subventral group was erratic, due chiefly to the absence of seta SV2 from either one, or both, sides of the body. This particular group was then examined on an additional 494 larvae and the variations to which it is liable are described and their frequency indicated.

The larvae examined comprised two collections, each from a different locality and food-plant. The degree to which the chaetotaxy varied in each collection was appreciably different.

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THE TARSAL CHEMORECEPTORS OF THE HOUSEFLY.

By V. G. DETHIER, Ph.D.

(*London School of Hygiene & Tropical Medicine.*¹)

UNTIL the appearance of the recent paper by Lewis (1954) all attempts to identify the tarsal chemoreceptors of the housefly (*Musca domestica*) had taken the form of morphological or histological studies unsupported by physiological tests. As a result of the earlier studies not a few erroneous conclusions were drawn; these were being perpetuated in the literature while the true identity of the chemoreceptors remained hidden. Because of the great interest in *Musca domestica* as an insect of medical importance and a test insect for insecticides, it seemed desirable to undertake with *Musca* a study comparable to those so successfully carried out with the blowflies *Protophormia terranova* (Lewis, 1952) and *Phormia regina* (Grabowski and Dethier, 1954). The present communication supplements the data presented by Lewis (1954). Except where noted, all types of hairs described have been shown by individual or group stimulation to be receptors which mediate responses to sucrose. Innervation was studied in preparations stained with methylene blue.

The tarsal chemoreceptors of *Musca* do not differ structurally from their counterparts on the legs of *Protophormia* and *Phormia*. They are blunt-tipped, thin-walled, socketed hairs equipped with two central lumina. The wall of one side of the hair is thin and transparent; that of the other side thick and pigmented. Intact hairs thus have a two-toned appearance. Four structurally different types corresponding to types A, B, C and D of *Phormia* occur. Type A is characteristically more blunt, thicker in proportion to its length, straighter and shorter than all other types. The difference is not so marked as in the case of *Phormia*. Type A hairs vary in length from 15 to 30 microns. They are restricted in distribution to the ventral surfaces of the tarsomeres. On the prothoracic and mesothoracic legs they are more or less evenly distributed over the ventral surface. On the metathoracic legs the A hairs are concentrated proximally on tarsomeres two to four and distally on five. In every case they are more or less scattered among the ventro-lateral B hairs although their distribution overlaps to a more ventral position.

Hairs of types B, C and D differ from A in possessing more acutely rounded tips and greater length. There is no outstanding characteristic which separates them from each other. Type D are the longest, ranging from 200 to 240 microns. Type C vary from 120 to 170 microns in length; type B, from 40 to 210. Since there is a continuous gradation in length from the shortest B to the longest C and since there are no real distinguishing characteristics or known physiological differences, it seems advisable to combine B and C into a single category. Accordingly, in the following description all such hairs will be referred to as B. The shorter B hairs frequently exhibit two flexures; the longer ones, as well as type D, have a single curvature. B hairs in a dorsal position and those on

¹ Permanent address, The Johns Hopkins University, Baltimore 18, Md., U.S.A.

the tibia and tarsus differ from all others in being somewhat more heavily pigmented. The largest groups of B hairs are found in ventro-lateral positions. On the prothoracic legs the concentration is distal on all segments except the first where there is, in addition to the distal group, a proximal group. On this segment there is also a striking proximal group of long B and D hairs in a ventral position. On the mesothoracic legs the B hairs are concentrated distally on the ventro-lateral surfaces of the tarsomeres five to two. On tarsomere one they are more evenly distributed. On the metathoracic leg they are concentrated distally on tarsomeres four and five, proximally on two and three and evenly distributed on one. Dorsally located B hairs on all legs are usually found in a distal position on all segments except the first, where they are evenly distributed.

The numerical distribution of two-toned hairs is shown in Table I which represents averages of counts of six legs of each thoracic segment. Although the absolute numbers do not agree in detail with those given by Lewis, they are of the same order of magnitude. The discrepancies are accounted for in part by the difficulty in distinguishing from among the densely packed hairs and spines those sensilla which are two-toned in appearance. The total numbers given here are greater because tibial chemoreceptors are included in these counts. With regard to the distribution of receptors the two studies are in good agreement. The total number of sensilla decreases from prothoracic leg to metathoracic; the greatest concentration of sensilla for any leg is on the second to fourth tarsomeres inclusive.

Of all types, B is the most numerous; A, the second most numerous. The total number of hairs increases in passing from the fifth to the second tarsomeres. The number is decreased on the first tarsomere. Type A hairs are generally absent on the first tarsomere. The distribution and relative numbers resemble those in *Phormia regina*.

With the exception of D type hairs all two-toned hairs have been shown by direct stimulation to be sensitive to sucrose. Again, with the exception of type D, the innervation of which has not been seen, the hairs are innervated by a maximum of three bipolar neurons. Some of the stouter heavily pigmented hairs and spines, which respond to mechanical stimulation, are innervated by a single large bipolar neuron. These tactile receptors are always thick-walled in comparison with the chemoreceptors.

These results are not in agreement with those of Sarkaria and Patton (1949) and Hayes and Liu (1947). The former have stated that epidermal sensory cells are only present in great abundance on the fifth tarsal segment. This is clearly not the case. Hayes and Liu have stated that chemoreceptors are absent from the first tarsomere and dorsal surfaces, and that only two are present on the second segment. The present study does not bear out these contentions. Furthermore, the hairs are not innervated by a large group of sensory cells. It is indeed true that each hair has associated with it a sac of five or six cells, but only three of these are neural. The remainder comprise the trichogen, the tormogen and an assortment of tracheal and neurilemma cells.

SUMMARY.

The legs of the housefly, *Musca domestica*, are clothed with large numbers of characteristically double-walled hairs which have been shown by direct individual and group stimulation with sucrose to be the tarsal chemoreceptors.

The structure, innervation, and distribution of these hairs are similar to those of the hairs in *Protophormia terranova* and *Phormia regina*. Each hair is innervated by three bipolar neurons and possesses two lumina. The hairs are most numerous on the prothoracic legs.

TABLE I.—*Distribution of two-toned hairs on the legs of Musca domestica*

Segment.	Prothoracic leg.			Mesothoracic leg.			Metathoracic leg.		
	A	B	D	A	B	D	A	B	D
5th Tarsomere :									
Dorsal . . .	.	2	.	.	2	.	.	2	.
Lateral . . .	.	4	2	.	2	2	.	.	2
Ventro-lateral . . .	.	22	.	.	20	.	.	14	.
Ventral . . .	.	8	2	.	8	.	4	.	.
Total each type . . .	8	30	2	8	24	2	4	16	2
Total all hairs . . .	40			34			22		
4th Tarsomere :									
Dorsal . . .	.	4	.	.	2	.	.	2	.
Lateral . . .	.	.	2	.	.	.	.	4	.
Ventro-lateral . . .	.	28	.	.	20	.	.	12	2
Ventral . . .	24	.	.	16	.	.	8	.	.
Total each type . . .	24	32	2	16	22	2	8	18	2
Total all hairs . . .	58			40			28		
3rd Tarsomere :									
Dorsal . . .	.	4	.	.	2	.	.	2	.
Lateral . . .	.	4	.	.	.	.	.	2	.
Ventro-lateral . . .	.	18	2	.	16	2	.	14	2
Ventral . . .	24	.	.	22	.	.	8	.	.
Total each type . . .	24	26	2	22	18	2	8	18	2
Total all hairs . . .	52			42			28		
2nd Tarsomere :									
Dorsal . . .	.	4	.	.	2	.	.	4	.
Lateral . . .	.	4	.	.	.	.	.	2	.
Ventro-lateral . . .	.	22	2	.	20	2	.	2	.
Ventral . . .	28	.	.	20	.	.	8	14	.
Total each type . . .	28	30	2	20	22	2	8	22	0
Total all hairs . . .	60			44			30		
1st Tarsomere :									
Dorsal . . .	.	2	.	.	8	.	.	6	.
Lateral . . .	.	2	.	.	.	.	.	4	.
Ventro-lateral . . .	.	28	2	.	14	.	.	.	.
Ventral . . .	.	3	1	6	2	.	.	10	.
Total each type . . .	0	35	3	6	24	0	0	20	0
Total all hairs . . .	38			30			20		
Tibia :									
Dorsal . . .	.	10	.	.	10	.	.	10	.
Ventral . . .	.	6	.	.	6	.	.	8	.
Total all hairs . . .	16			16			18		

TABLE I—continued.

Segment.	Prothoracic leg.			Mesothoracic leg.			Metathoracic leg.		
	A	B	D	A	B	D	A	B	D
Femur :									
Dorsal . . .	.	.	.	.	.	.	.	.	.
Ventral . . .	.	4	.	.	2	.	.	6	.
Total all hairs . . .	4			2			6		
Totals	84	173	11	72	128	8	28	116	6
Grand totals	268			208			150		

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BOOK NOTICE.

Applied Entomology. An Introductory Textbook of Insects in their Relations to Man. By H. T. FERNALD and HAROLD H. SHEPARD. McGraw-Hill Publications in the Agricultural Sciences. 8vo. London & New York (McGraw Hill), 5th edition. 1955. Pp. ix + 385, text illust. Price \$7.00.

This is the fifth edition of a work which first appeared in 1921, and is intended to introduce entomology to students of agriculture and associated pursuits. The introductory chapters deal with general aspects of the subject (anatomy, physiology and development), and then the economic importance of insects is discussed, with sections on natural and applied control.

The last edition appeared in 1942 and the section on insecticides has been extensively revised to include information on the new insecticides which have revolutionised the control of many insects.

In the remainder of the work the classification of insects is emphasised, generally using as examples species which are well known as being either very harmful or very beneficial. Specific control measures are included for injurious forms.

The final chapter deals with pest animals other than insects.

Less essential illustrations have been omitted from the new edition and many new ones inserted. An index completes the work.

THE NYMPHS OF THE BRITISH SPECIES OF *CAPNIA* (PLECOPTERA).

By H. B. N. HYNES, Ph.D., F.R.E.S.

(Department of Zoology, University of Liverpool.)

WHEN I wrote my paper on the classification of the nymphs of British stoneflies (Hynes, 1941) of the three species in the genus *Capnia* only the young stages of *C. bifrons* (Newman) (= *C. nigra* of most British authors, Kimmins 1947) were available. It was, however, possible to predict that fully grown male nymphs of *C. atra* Morton would be distinguishable because, in this country, this is the only species in which the adult male is fully winged.

Brown (1945) reported the discovery of nymphs of *C. atra* in Scotland, and gave characters by which well-grown male nymphs of *C. atra* and *C. bifrons* could be distinguished. These were the well-developed wing-pads in the former and the shape, as seen in profile, of the tenth tergum. He was unable to find any method of distinguishing the females, and had difficulties because he was working with a mixed population of *C. atra* and *C. bifrons* and so could not be certain of the identity of many of his specimens.

Previously no author had attempted to distinguish nymphs of species in this genus, although several descriptions of the nymph of "*C. nigra*" had been published (references in Hynes, 1941). In view of the uncertainty of the nomenclature before the publication of Aubert's (1946) work these descriptions may be of either *C. bifrons* or *C. nigra* (Pictet) (= *C. conica* Klapálek, the nymph of which was described by Kütreiber 1931).

Aubert (1946), working in Switzerland, gave characters separating the nymphs of *C. bifrons* (*sub nom. quadrangularis* Aubert) and *C. nigra* s.s., but, as the latter does not occur in Britain, this did not enable identification of British nymphs. Neither did it indicate the sort of character by which *Capnia* nymphs would prove to be separable because Brinck (1949) pointed out that most of the characters proposed by Aubert were unreliable, and those that remained were applicable only to well-grown male nymphs.

Brinck (1949), working in Sweden, was the first to give a key to the nymphs of several species. Of these *C. atra* and *C. bifrons* occur in Britain. The characters he proposed for separation of these species were the presence of a pair of long stout bristles on each side of the metanotum of *C. atra*, the differing shapes of the tip of the abdomen and development of the wing-pads in well-grown male nymphs, and the presence in *C. atra* of a strongly chitinated vulva in ripe female nymphs. Only the first of these is a truly nymphal character, and, unfortunately, it has been found to be inapplicable in Britain. Many British nymphs of *C. bifrons* also possess a pair of long bristles on the metanotum, although these are less well-developed than in *C. atra* and I have seen similar small bristles on some nymphs of *C. bifrons* from southern Sweden.

Finally Aubert (1951) described the nymph of *C. vidua* Klapálek from Switzerland. This is the third British species. He stated that it was distinguishable

from *C. bifrons* by its greater hairiness and longer pronotal bristles, and by the shape of the tenth tergum in well-grown male nymphs.

In effect, therefore, the only characters available from the literature for separating the nymphs of the three British species are :

- (1) The shape of the tenth tergum in well-known male nymphs.
- (2) The fully developed wing-pads in well-grown male nymphs of *C. atra*, as opposed to small wing-pads in *C. bifrons* and *C. vidua*.
- (3) The heavy chitinisation of the vagina in ripe female nymphs of *C. atra*.
- (4) The greater hairiness of *C. vidua* than of *C. bifrons*, and the longer pronotal bristles of the former.

Of these, the first three are clearly almost adult structures, and can only apply to nymphs not far from emergence, and the last is too vague a character to use with confidence, especially as it undoubtedly varies with the size of the nymphs. It has, in fact, proved not to apply clearly in Britain, as it apparently does in Switzerland, even to well-grown nymphs.

In April 1953, Mr. H. Whitehead of Leeds gave me two adults, a nymph and a nymphal skin of *C. vidua* collected by Professor Percival in 1929 in Maize Beck, Upper Teesdale. It was possible, because of the shape of the tenth tergum, to be certain of the identity of the nymphal material. I knew that Mr. E. S. Brown of the Commonwealth Institute of Entomology possessed British material of *C. atra*, and I have much material of *C. bifrons* from various parts of the country. I resolved, therefore, to attempt to find truly nymphal characters by which the nymphs of the three British species could be distinguished. Accordingly I borrowed the material on which Mr. E. S. Brown's (1945) paper was based, and I also obtained some Swedish nymphs of *C. atra* from Dr. P. Brinck of Lund. Mr. E. S. Brown later informed me that Mr. V. M. Brown of Durham University was working on a population of *C. vidua* in Upper Teesdale, and the latter has also kindly supplied me with nymphs of this species. To all these gentlemen I wish to offer my sincere thanks for their great help, without which this work could not have been done. To Dr. Brinck I am further indebted for checking my provisional key on Swedish specimens in his collection.

COMPARISON OF THE NYMPHS.

Examination of the nymphs of all three species showed them to be extremely similar to one another, apart from the shape of the tenth tergum in well-grown males, and the full development of the wing-pads in *C. atra*. No structural differences were found between them, despite thorough examination. Differences which were apparently constant were, however, found in the lengths and detailed arrangement of the bristles.

The general arrangement of setae in all three species is the same (figs. 1 and 2). The antennae bear a few small spines on the basal half, and these decrease in size distally. The cerci bear a few scattered bristles on the basal segments, and each segment, except the first few, bears distally one long hair dorsally and one ventrally, which together form fringes along the cerci. The mouth parts bear scattered clothing hairs. The legs have a general cover of clothing hairs, and there are bristles along the front and hind margins of the femora. The tibiae also bear a few spines posteriorly, and along the posterior borders are fringes of long hairs which extend on to the tarsi. The body has a general cover of fine clothing hairs, which are more numerous dorsally. In addition,

there are a number of longer upstanding hairs along the dorsal and posterior part of the ventral surfaces. On the head there are pairs of such hairs between the antennal bases, between the eyes and on the vertex. There is a similar pair lying one on each side of the suture on the anterior and posterior borders

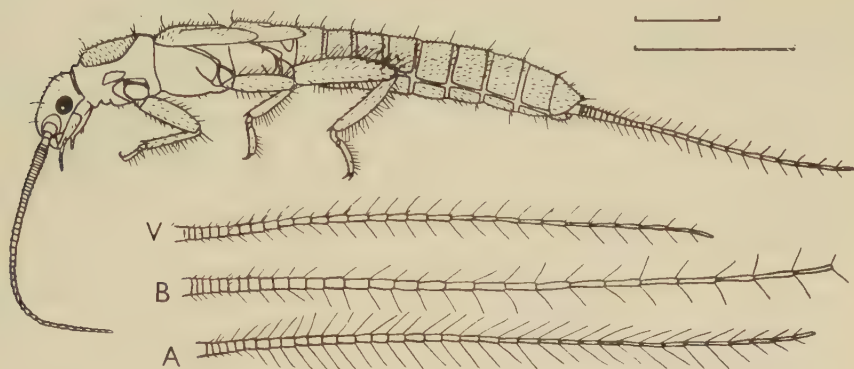


FIG. 1.—Fully grown female nymph of *C. bifrons* in lateral view, and cerci of *C. atra* (A), *C. bifrons* (B) and *C. vidua* (V) in lateral view. The lines represent 1 mm., the lower being the scale to which the cerci are drawn.

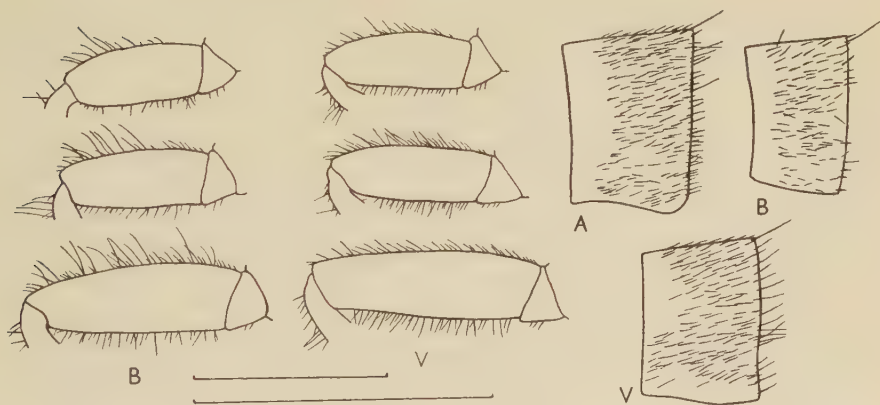


FIG. 2.—Femora, as seen in silhouette, of full grown nymphs of *C. bifrons* (B) and *C. vidua* (V), and fifth abdominal terga, as seen in lateral view, of fully grown nymphs of *C. atra* (A), *C. bifrons* (B) and *C. vidua* (V). The terga are drawn from cleared specimens. The lines represent 1 mm., the lower being the scale to which the terga are drawn.

of the nota. This series is continued on the posterior borders of the abdominal terga, and is present also on some of the posterior abdominal sterna. Each sclerite has a fringe of hairs posteriorly, and some of these may be long, almost as long as the upstanding hairs. On the abdominal terga some of these longer hairs may form a second pair of long hairs lateral to the median pair. All these

hairs and bristles are difficult to see in cleared and mounted specimens, but show up well in preserved specimens when these are examined in profile against transmitted light of low intensity.

The series of long upstanding hairs varies somewhat in development, but some of them are always present. They are perhaps most obvious in *C. atra* and least in *C. vidua*. It was the anterior metanotal pair of the series that Brinck used for separation of *C. atra* and *C. bifrons*.

Differences which were found between the species are listed below. As regards *C. atra*, these were worked out on Swedish specimens, as much of Mr. E. S. Brown's material was either mounted in balsam or not certainly identified. Each point was, however, carefully checked on the British material. All the figures were drawn with the aid of a projector, and all the figures of *C. atra*, except the abdominal tergum of fig. 2, were drawn from Swedish specimens, because no suitable unmounted British material was available.

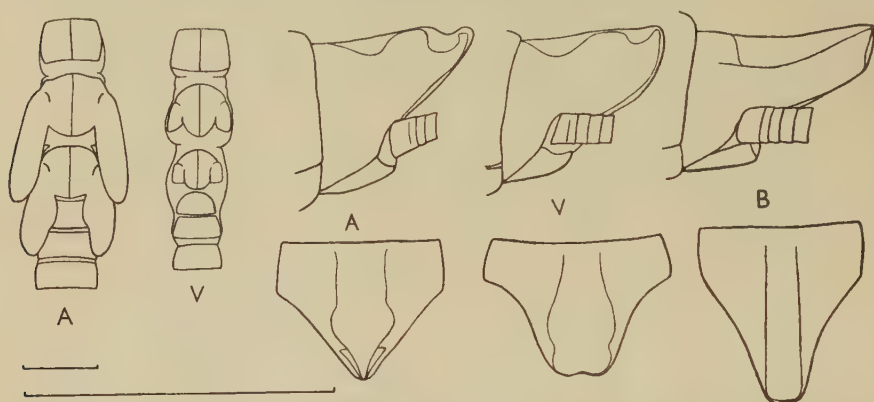


FIG. 3.—Thoraces of fully grown male nymphs of *C. atra* (A) and *C. vidua* (V), and tenth abdominal segments of ripe male nymphs of *C. atra* (A), *C. bifrons* (B) and *C. vidua* (V) in lateral and dorsal view. The outlines of the supra-anal lobes of the adults are seen through the nymphal cuticles. The lines represent 1 mm., the lower being the scale to which the tenth segments are drawn.

(1) The clothing hairs are longer and denser in *C. atra* and *C. vidua* than in *C. bifrons* (fig. 2). This is not a character which can be used with certainty, as the length of these hairs decreases relatively as the nymphs increase in size. No specimens of *C. vidua* were seen in which the prothoracic hairs were as long as described by Aubert (1951), but this may represent a racial difference between *C. vidua vidua*, which Aubert was describing, and *C. v. anglica*, which is the British sub-species (Aubert 1950).

(2) The hairs forming the cercal fringe are much longer in *C. atra* than in the other two species (fig. 1). This applied to the Swedish material and all the certainly identified British nymphs which still retained their cerci. It apparently does not apply to very small nymphs of *C. atra* (see below), but for larger nymphs it is probably a reliable character.

(3) In *C. bifrons* the bristles along the hind margins of the femora are mostly longer than those along the front margins. They are about equal in length in

the other two species. This is shown in fig. 2, where the femora are drawn as silhouettes, i.e. only those bristles are shown which project beyond the margin of the limb. This character applies to all nymphs of *C. bifrons* and *C. vidua* longer than about 6 mm., below which size it does not apply: no small nymphs of *C. atra* have been examined.

(4) In nymphs of *C. bifrons*, but not of the other two species, there is on each tergum a pair of small upstanding hairs beside the mid-line about half-way along the length of the tergum. These are about half the length of the long upstanding hairs (fig. 2). These occur in large and quite small nymphs (4–5 mm.) of *C. bifrons*, and are easily seen in profile. In some specimens there is a second similar pair more laterally. This characteristic feature is rendered very difficult to see by clearing and mounting, because the hairs change their position, and the short upstanding hairs closely resemble the ordinary clothing hairs.

In addition to these characters fully grown male nymphs can be readily identified by the shape of the tenth tergum and the underlying supra-anal lobe (fig. 3), and by the full development of the wing-pads in *C. atra*. Males of *C. bifrons* have very short wings as have males of the British race of *C. vidua* (fig. 3). Fully grown female nymphs of *C. atra* have a strongly chitinated vulva on the eighth abdominal sternum; this is not found in the other two species.

On the basis of these characters the following key has been constructed, but it should be emphasised that identification of these nymphs is not easy, and that as in the genera *Leuctra* and *Nemoura* (Hynes 1941) several specimens from each locality should be studied.

KEY TO NYMPHS OF BRITISH SPECIES OF *Capnia*.

1. Hairs of dorsal and ventral fringe on cerci long; in the middle of the cerci considerably longer than the segments (fig. 1). Wing-pads of fully grown male nymph well developed (fig. 3). 10th tergum of well-grown male nymph pointed in dorsal and lateral view and emarginate dorsally (fig. 3). 8th sternum of ripe female nymph with a heavily chitinated vulva. (Femora and abdominal terga as in *C. vidua*). In Britain a lake shore species *C. atra* Morton
- . Hairs of dorsal and ventral fringe on cerci shorter; in the middle of the cerci as long as or shorter than the segments (fig. 1). Wing-pads of fully-grown male nymph rudimentary (fig. 3). 10th tergum of well-grown male nymph not pointed and not emarginate dorsally (fig. 3). 8th sternum of ripe female nymph without a heavily chitinated vulva. 2
2. Bristles along posterior borders of femora longer than those along anterior borders (fig. 2). Each abdominal tergum with a pair of short upstanding hairs about half-way along the mid-dorsal line (fig. 2). 10th tergum of well-grown male nymph truncated in lateral view (fig. 3). Streams and lake shores *C. bifrons* (Newman)
- . Bristles along posterior borders of femora about the same length as those along anterior borders (fig. 2). No short upstanding hairs half-way along abdominal terga (fig. 2). 10th tergum of well-grown male nymph broadly rounded posteriorly (fig. 3). Streams . *C. vidua* Klapálek

This key will serve to separate nymphs of *C. vidua* and *C. bifrons* longer than about 6 mm., and Dr. Brinck has checked it for me on further Swedish material of *C. atra* and *C. bifrons*. It is, however, uncertain how far it will apply to partly grown nymphs of *C. atra*. Neither Dr. Brinck nor I possess half-grown

nymphs of this species, and Dr. Brinck has found that in very small nymphs (2–3 mm.) the hairs of the cercal fringe are shorter than the segments. In Britain, however, it seems that *C. atra* is entirely lacustrine, so it is only likely to be confused with *C. bifrons*. From this species young nymphs of *C. atra* will almost certainly prove to be separable on the absence of the short upstanding hairs of the abdominal terga and the relative lengths of the femoral bristles.

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BOOK NOTICE.

The Megachiline Bees of California (Hymenoptera : Megachilidae). By PAUL D. HURD, JR., and CHARLES D. MICHENER. Bulletin of the California Insect Survey. 3. Large 8vo. California (University of California Press) and London (C.U.P.), 1955. Pp. iv + 248, 24 pls., 112 maps, tab. Price \$3.50.

This work, which forms Volume 3 of the Bulletin of the California Insect Survey, attempts to provide descriptive keys and detailed distributional data of certain of the megachiline bees found in California. The genera *Anthocopa*, *Ashmeadiella*, *Chelostoma*, *Chelostomopsis*, *Diceratomia*, *Heriades*, *Hoplitis*, *Proterialdes* are treated in detail, but the genera *Coelioxys*, *Megachile*, and *Osmia* are considered only to the subgeneric level.

The text is printed in double column and is very fully illustrated. An index of species and one to floral visitational records complete the work.

THE LARVAL INSTARS OF SOME GALL MIDGES OF THE GENUS
THOMASINIANA STRAND, E., 1916 (DIPTERA : CECIDOMYIDAE).

By R. S. PITCHER.¹

(East Malling Research Station, Kent.)

THE genus *Thomasiniana* at present contains seven described species. All except one (*T. salvadorae* Rao) occur in Europe and, although classed as gall midges, live under peeling or broken surface tissues of the host plant, causing local death of cells, but no proliferation. Attention was first directed to the larval instars of this genus in the course of biological studies on *T. theobaldi* (Pitcher, 1952). The observations then made have since been extended, although in rather less detail, to cover the other species known to live on Rosaceous host plants. A brief account of their biology is given below.

T. oculiperda (Rübs.) has been known since 1881 as a pest of newly budded roses and fruit trees, which its larvae damage by feeding on the cambial layers of stock and scion (Barnes, 1931). *T. theobaldi* Barnes is a pest of raspberries ; its larvae feed between the epidermis and periderm and in so doing render the cane liable to attack by fungal pathogens (Pitcher and Webb, 1952). *T. crataegi* Barnes lives on hawthorn, and damages the cambium, often causing die-back of shoots (Barnes, 1939). *T. fruticosi* Pitcher lives on wild blackberry canes, sometimes under peeling epidermis, but more usually in cut or broken areas (Pitcher, 1955).

Although the literature on the biology and morphology of the Cecidomyiidae is extensive, it seems that comparatively little is known of the larval moults and instars. In *Phytophaga destructor* (Marchal, 1897) and *Oligotrophus oleariae* (Anderson, 1935) three phases—migratory, feeding and prepupal—have been described ; one or more moults occurring during the feeding phase. Chaîne (1913) could discern no moults in *Monarthropalpus buxi*, but Hamilton (1925) and Ries (1937) found four. Four instars have also been recorded in *Dasyneura leguminicola* (Metcalf, 1933), *Rhabdophaga saliciperda* (Sen, 1938) and *Dasyneura lini* (Pruthi and Bhatia, 1937) ; Couderc (1933) observed five in *Perrisia affinis*, but Melis (1938) only three in *Perrisia pyri*.

Most authors agree that newly hatched larvae have a simple respiratory system and that fully fed larvae are armed with a sternal spatula. The intermediate stages, however, have usually been defined in a rather arbitrary manner, often being distinguished only by body size and colour and by indefinite details of chaetotaxy and epidermal texture. In the writer's experience the former are characters which change gradually and cannot be clearly assigned to any one instar, while the latter require more precise definition to be of any diagnostic value. Apparently no attempt has been made to apply Dyar's Law to the head capsule width of Cecidomyiids, but the writer has found it to hold good for the larvae of a Mycetophilid, *Sciara fenestralis* Zett. (Pitcher, 1936).

¹ Including some data already presented in a Thesis approved for the Degree of Doctor of Philosophy in the University of London.

*T. theobaldi.**External Morphology of Larva.*

Newly hatched larvae are translucent and barely visible to the naked eye, approximately 0.4×0.095 mm. in size; fully fed larvae may reach a size of 3.4×0.9 mm. and are either pink or orange in colour. At all stages the larvae are apodous, tapering towards either end. The small prognathous head capsule bears reduced mouthparts in a bluntly conical extension at its apex and a pair of antennae on its dorsal surface. The body consists of thirteen segments, one supernumerary, three thoracic and nine abdominal. The supernumerary segment bears no setae; the thoracic and the first seven abdominal segments each bear six setae on the dorsum and a pair of lateral setae on either margin.

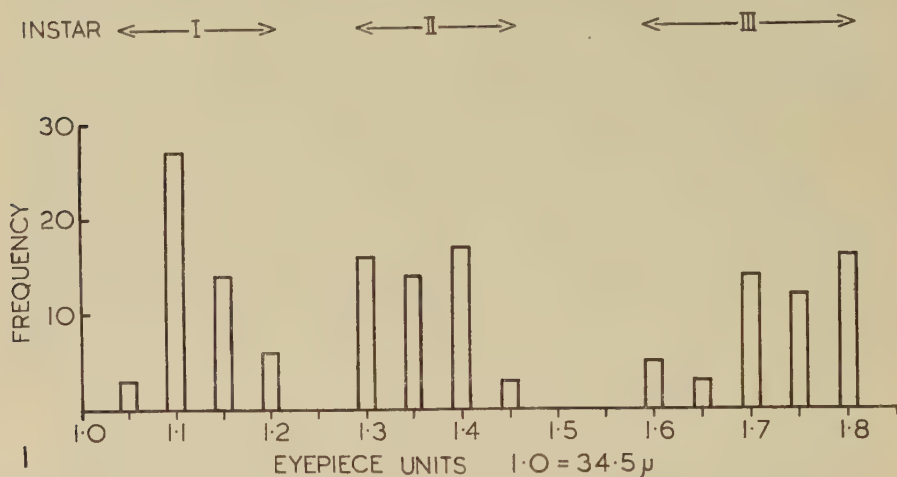


FIG. 1.—Histogram of head capsule widths of larvae of *Thomasiniana theobaldi*.

On the eighth abdominal segment the lateral setae are similarly arranged, but there are only two stout dorsal setae. The posterior margin of the ninth abdominal segment is deeply indented, each half terminating in a stout upcurved process. In addition each half bears three small setae, one dorsally, one laterally and one, the smallest, on the inner margin. Most of the segments bear transverse patches of very small backwardly projecting spines, which appear to aid locomotion, being most marked on the ventral surface. On the anterior and posterior segments, however, they are either scarce or absent.

Instars.

Measurement of the head capsule widths of larvae obtained from the field showed that there were three clearly defined size groups (fig. 1). The possibility that each group consisted of larvae of a single instar was further explored by morphological examination. Consideration of the two characters most commonly mentioned by other workers, namely the respiratory system and the sternal spatula, soon showed differences which corresponded to the head capsule size groups. Thus the respiratory system was metapneustic in the size group

1.05 to 1.20 units inclusive and peripneustic in the others, while the sternal spatula was present only in the size group 1.60 to 1.80 units inclusive. Closer examination revealed the other consistent morphological differences listed in Table I, which is based on a sample of fifty individuals of each group.

TABLE I.—*Comparative Morphology of Larval Instars of T. theobaldi.*

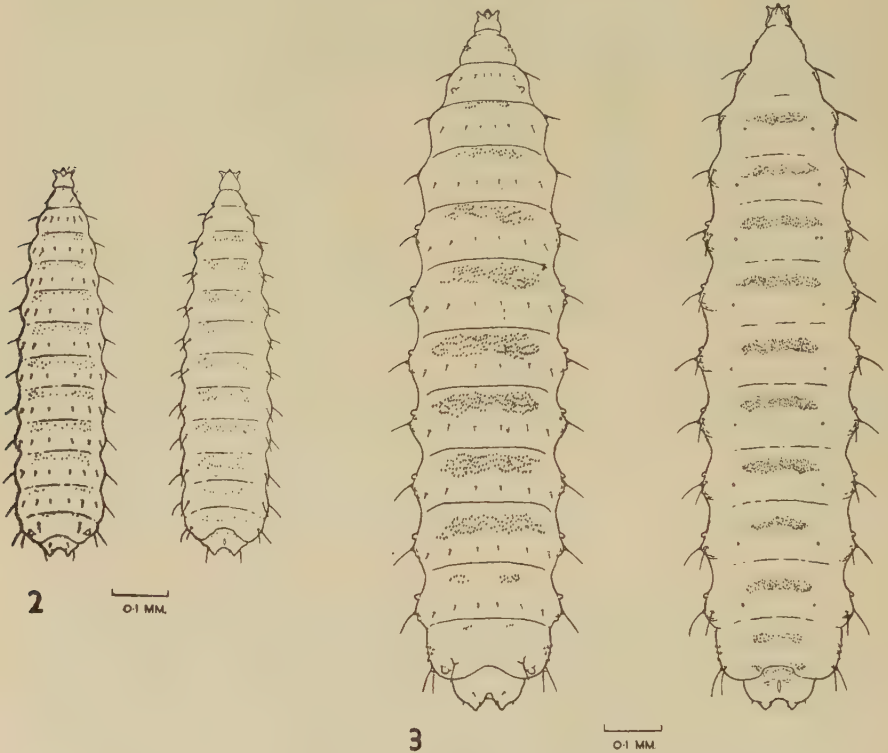
		Instar I.	Instar II.	Instar III.
Body length (mm.)	. Min.	0.29	0.80	1.62
" "	. Avge.	0.61	1.20	2.78
" "	. Max.	0.80	1.70	3.56
Body width (mm.)	. Min.	0.08	0.17	0.51
" "	. Avge.	0.16	0.31	0.74
" "	. Max.	0.24	0.51	0.99
Head capsule width (μ)	Min.	36.2	44.8	55.1
" "	. Avge.	38.5	46.9	59.5
" "	. Max.	41.4	50.0	64.0
Respiratory system	. —	Metapneustic	Peripneustic	Peripneustic.
Sternal spatula	. —	Absent	Absent	Present.
Epidermis	. —	Smooth, spines weak	Smooth, spines moderate	Papillate, spines strong. Ventral pseudopods.
Lateral spines on supernumerary segment	. —	One, stout	4-9, small	None.
Length of lateral abdominal setae	. —	Long, $\approx 17\%$ body width. All approx. equal	Moderate, $\approx 9\%$ body width. Shorter on posterior segment	Short, $\approx 3\%$ body width. Shorter on posterior segment.
Body colour	. —	Translucent-white	White	Pink or orange.

It will be seen that the figures of body size do not fall into discrete groups, but that those of head capsule width do, and, moreover, that they conform approximately to Dyar's Law, with an average ratio between instars of 1 : 1.24. Examination of larvae in the prepupal phase produced no evidence of a further moult within the cocoon as described by Melis (1938) in the case of *Perrisia pyri*. It was therefore concluded that the larvae of *T. theobaldi* pass through three clearly defined instars. Confirmation of this has been obtained by observing moults in larvae kept under laboratory conditions. In every case the morphological changes were those which were to be expected from the data given in Table I. Before moulting, the larvae enter an immobile resting phase in which the body becomes turgid. At this stage it is often possible to discern the characters of the forthcoming instar through the old larval skin. Figs. 2-4 show typical examples of larvae of each instar.

Under normal conditions of nutrition each instar lasts 3-5 days. In poor conditions feeding times may be prolonged and in a few individuals the head capsule widths may be atypical. With a little practice instar III larvae can be distinguished by eye because of their body colour and "matt" surface. Instars I and II are less easy to separate, but body size will suffice in all but borderline cases, for which a low power examination of a temporary mount may be needed.

T. oculiperda, *T. fruticosi* and *T. crataegi*.

The larvae of all three species are very similar to those of *T. theobaldi* and all go through three closely comparable instars. Head capsule widths fall into three groups in each case, and the other characters, e.g. respiratory system, sternal spatula, epidermal texture and spines on the supernumerary segment change with the moult as in *T. theobaldi*. Table II gives average dimensions of samples of not less than twenty-five individuals of each species.



FIGS. 2-3.—Larva of *Thomasiniana theobaldi*. (2), instar I. (3), instar II.

TABLE II.—Average Dimensions of Larval Instars of *Thomasiniana* spp.

		Instar I.	Instar II.	Instar III.
<i>T. oculiperda</i> (ex apple)	{ Body length (mm.)	0.52	1.52	2.48
	{ Body width (mm.)	0.12	0.39	0.56
	{ Head caps. width (μ)	38.20	46.00	57.00
<i>T. fruticosi</i>	{ Body length (mm.)	0.62	1.10	2.43
	{ Body width (mm.)	0.15	0.27	0.57
	{ Head caps. width (μ)	38.60	48.60	58.00
<i>T. crataegi</i>	{ Body length (mm.)	0.71	1.33	2.97
	{ Body width (mm.)	0.17	0.34	0.73
	{ Head caps. width (μ)	36.30	43.10	55.30

There are slight differences from species to species in the average length of some of the abdominal setae, and in the relative length of those on certain segments. This is especially so in the case of *T. crataegi* which can be separated from the other species on setal characters and by the paler pink colour of instar III larvae (Pitcher, 1955).



FIG. 4.—Larva of *Thomasiniana theobaldi*, instar III.

SUMMARY.

An account is given of the occurrence of three larval instars in four species of the genus *Thomasiniana*, namely *T. theobaldi*, *T. oculiperda*, *T. fruticosi* and *T. crataegi*. Differences in head capsule width, respiratory system, epidermal

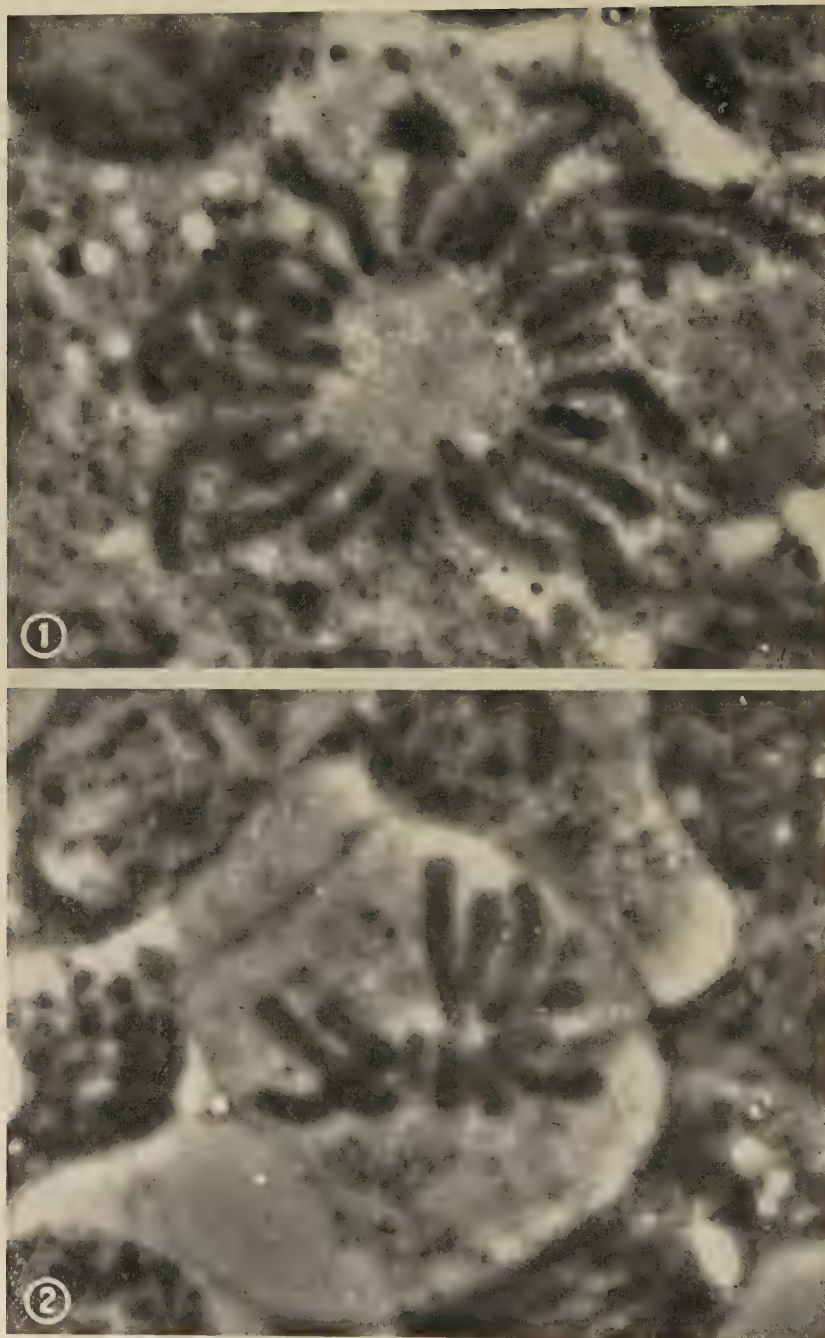
texture, sternal spatula development and other characters enable the instars to be clearly distinguished.

ACKNOWLEDGEMENTS.

The writer wishes to thank Dr. A. M. Massee and Dr. H. F. Barnes for their interest and assistance in this study.

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Parthenogenesis in the Desert Locust.

FIG. 1.—Phase contrast micro-photograph of a living cell from a parthenogenetically produced embryo showing the diploid number of chromosomes ($\times 2500$).

FIG. 2.—Phase contrast micro-photograph of a living cell from a parthenogenetically produced embryo showing the haploid number of chromosomes ($\times 2500$).

A. G. Hamilton.

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PARTHENOGENESIS IN THE DESERT LOCUST (*SCHISTOCERCA GREGARIA* FORSK.) AND ITS POSSIBLE EFFECT ON THE MAINTENANCE OF THE SPECIES.

By A. G. HAMILTON, D.Sc., Ph.D., B.Agr., F.R.E.S.

(*Biological Department, St. Thomas's Hospital Medical School, London, S.E.1.*)

1. INTRODUCTION.

ALTHOUGH a belief in parthenogenesis has existed since early times it was not, according to Peacock (1944), until 1667 that Goedart recorded his experiments on parthenogenesis.

Parthenogenesis occurs more often among insects than any other class of animals. There are three main types depending upon the sexes of the offspring which develop from the unfertilised egg: (1) arrhenotokous—males only (fertilised eggs giving rise to females); (2) thelytokous—females only; (3) amphitokous—both sexes. Most of the evidence seems to indicate that it is the thelytokous type which occurs sporadically in some Acrididae.

Among the Acrididae parthenogenesis has been recorded in *Locusta migratoria* (5 females) by Plotnikov (1915); in *Apotettix eurycephalus* (4470 females to 7 males) by Nabours (1919); in *Locustana pardalina* (not sexed as they were not reared to the adult stage) by Faure (1923); in *Paratettix texanus* (with rare exceptions all females) by Nabours and Foster (1929); in *Melanoplus differentialis*, *Arphia sulphurea*, *Hippiscus apiculatus* and *Trimerotropis citrina* (all females) by Slifer and King (1932); in *Melanoplus differentialis*, *Romalea microptera*, *Arphia sulphurea*, *Dissosteira carolina* and *Hippiscus apiculatus* (sex not stated but believed to be females) by King and Slifer (1934); in *Schistocera flavofasciata* (died during nymphal stage, sex not stated) by Kevan (1943); and in *Schistocerca gregaria* by Husain and Baweja (1936) and Norris (1952) who mention that parthenogenesis may occur but do not seem to have investigated its possibilities, by Hamilton (1953) who reared four successive generations, (all females), and by Norris (1954) who discontinued her experiments after some progeny (all females) had been produced. Husain and Mathur (1945) claim to have obtained one generation of this species parthenogenetically with equal numbers of males and females.

I would like to thank the Anti-Locust Research Centre for my original stock of locusts. Also I would like to thank Mr. A. G. Dinnes of the Biological Department for technical assistance and the staff of the Photographic Department of St. Thomas's Hospital Medical School for assistance and advice with the photographic work.

2. MATERIAL AND METHODS.

My locusts were kept in cages lined with asbestos, and covered externally, so that the walls had cavities giving good insulation. Each cage was divided into two compartments by a horizontal sheet of perforated zinc. The upper compartment measured approximately 19 in. long, 14 in. wide and 13 in. high.

The electric bulb (25 watts) for light, the thermostat (a Satchwell QP Room thermostat), an Edney Paper hygrometer, and the locusts were kept in this compartment. The lower compartment contained the heater (75 watts tubular "Sung" car heater) with a spreader above so that the hot air diffused through the perforated zinc into the upper compartment, a tray of sand, and a jar of water to regulate the relative humidity. Each compartment had a separate door. Tubes 4 in. long by $1\frac{1}{2}$ in. wide, containing sand for oviposition, were inserted flush with the zinc floor of the upper compartment.

My original stock of locusts was supplied by the Anti-Locust Research Centre and was reared in my laboratory for several generations before being tested for parthenogenetic reproduction. The females of the parental generation (Tables I and III) tested for parthenogenetic reproduction were separated from males while in the hopper stage. Females reproducing parthenogenetically were kept in a separate room with its own exterior entrance so there was no possibility of any contamination from my ordinary breeding stock, which were kept in the main part of the building.

Most of my experiments were carried out at a constant temperature of 90° F. (32.2° C.) and at a relative humidity of 60–70 per cent., but as work progressed it was decided to try alternating conditions which would be more akin to conditions in the field. In these experiments the temperature was 100° F. (37.8° C.) during the day and laboratory temperature (approximately 65° F.) during the night. All the above conditions have been shown to be suitable for this species (Hamilton, 1950).

Preparations for chromosome counts and micro-photographs were obtained by dissecting the developing embryos from the eggs after three to six days' incubation. This was done in Ringer's solution under the stereoscopic binocular microscope. The embryos were carefully removed from the yolk, placed on a slide and a drop of glucose solution added. They were then covered with a cover-glass which was firmly pressed down (using a filter-paper) to give a squash preparation. The preparation was then ringed with nail varnish to prevent evaporation. The micro-photographs were taken on a Leitz's Dialux microscope fitted with Phase Contrast Equipment.

3. ADULTS.

(a) *Rate of Sexual Maturation.*

The period between the emergence of the adults and the production of the first egg-pod is taken as the standard for measuring the rate of sexual maturation. In Table I it can be seen that in experiment No. 1 females reproducing parthenogenetically at 90° F. and relative humidity of 60 to 70 per cent. required considerably longer (35 days) to reach sexual maturation than in the case of the controls (22 days) where copulation occurred. In experiment No. 2 the difference was not so great, but if the average of the two sets of experiments is taken, then there is sufficient evidence to suggest that either copulation or the presence of males in the cage speeds up the rate of sexual maturation of the females. In the case of experiment No. 3, where conditions of temperature and relative humidity were different during the day and night, the time required to reach sexual maturation was only two days longer for females reproducing parthenogenetically than for those reproducing sexually.

(b) *Length of Adult Life.*

The difference in the length of adult life of females reproducing parthenogenetically compared with those reproducing sexually is, perhaps, one of the most outstanding features of parthenogenesis. On the average, the length of adult life of the former is three times greater than the latter, thus suggesting that the metabolic rate is much slower.

(c) *Fecundity.*

The accepted standard of fecundity is the total eggs per female. Taking first the number of egg-pods per female, it was found that the parental stock of females reproducing parthenogenetically gave a higher average number of egg-pods than those reproducing sexually (Table I), but if the number of egg-pods produced by the successive generations reproducing parthenogenetically (Table III) is considered, then there is little difference. When the number of eggs per egg-pod is correlated with the number of egg-pods it can be seen from the tables that there is really no significant difference in the total number of eggs per female.

TABLE I.—*Comparison of the rate of sexual maturation, the length of adult life, and fecundity in Schistocerca gregaria reproducing parthenogenetically and sexually.*

Type of Reproduction	Experiment No. 1.		Experiment No. 2.		Experiment No. 3.	
	Started September, 1952. Constant temp. of of 90° F. Rel. hum. 60-70%.		Started September, 1953. Constant temp. of of 90° F. Rel. hum. 60-70%.		Started November, 1953. Temp.: 100° F. during the day and lab. temp. during the night. Rel. hum. 45-80%.	
	Partheno- genetic.	Sexual. (Control).	Partheno- genetic.	Sexual. (Control).	Partheno- genetic.	Sexual. (Control).
Number of males . . .	0	8	0	6	0	9
Number of females . . .	10	10	10	10	10	10
Length of adult life of females } (in days) {	Average	182.1	63.5	258.4	68.3	218.3
	Minimum	97	26	156	36	127
	Maximum	328	168	339	108	289
First egg-pod (in days) . . .	35	22	25	21	26	24
Last egg-pod (in days) . . .	320	102	317	107	213	85
Average egg-pods per female . . .	5.4	3.5	5.6	4.6	5.2	2.6
Average days per egg-pod . . .	33.7	18.1	46	14.8	40.4	22.6
*Average eggs per egg-pod . . .	42.8	47.2	41.2	40.0	46.0	39.7
*Average number of hoppers which hatched per egg-pod . . .	10.1	35.5	8.5	33.1	6.2	33.7
Percentage of eggs which hatched . . .	23.6	75.2	20.6	80.4	13.4	85.1
Average incubation period (in days)	14.2	14.1	14.1	14.7	22.7	21.2

* Calculated from approximately 10 egg-pods which had yielded a hatch.

TABLE II.—*Hopper development and sex ratio of parthenogenetically and sexually produced hoppers of Schistocerca gregaria at 90° F. (32.2° C.) and at 60–70 per cent. relative humidity.*

	How produced.		
	From eggs laid parthenogenetically.	From eggs laid by parthenogenetically produced females F ₄ after mating.	From eggs laid by ordinary stock females after mating. (Controls.)
Number of hoppers . . .	271*	68*	232*
Average length of hopper life (in days) . . .	29.2	26.8	28.6
Percentage of hoppers reaching the adult stage . . .	34.7	48.5	52.2
Sex of adults { Males . . .	0	17	56
{ Females . . .	94	16	65

* These figures are the combined results from a number of experiments.

TABLE III.—*Parthenogenetic reproduction for 5 successive generations in Schistocerca gregaria.*

	Generation.					
	Parental.	F ₁ .	F ₂ .	F ₃ .	F ₄ .	F ₅ .
Time required for hopper development (in days) . . .	29.3	32.7	28.7	29.5	28.5	34.3
Number of adults (females) . . .	10	8	15	10	10	3
Length of adult life of females (in days) { Average . . .	182.1	130.5	91.4	161.1	136.4	107.1
{ Minimum . . .	97	33	21	104	100	49
{ Maximum . . .	328	226	167	225	166	184
First egg-pod (in days) . . .	35	37	31	30	41	28
Last egg-pod (in days) . . .	320	211	157	200	144	138
Average egg-pods per female . . .	5.4	3.1	2.4	2.3	2.9	2.8
Average days per egg-pod . . .	33.7	36.9	38.1	70.0	37.6	40.4
*Average eggs per egg-pod . . .	42.8	40.1	47.0	41.3	42.5	46.8
*Number of hoppers which hatched per egg-pod { Average . . .	10.1	10.6	10.3	11.5	10.2	13.1
{ Minimum . . .	1	1	4	3	3	4
{ Maximum . . .	35	30	21	20	16	26
Percentage of eggs which hatched . . .	23.6	26.3	25.5	27.8	23.8	28.0
Average incubation period (in days) . . .	14.2	14.7	14.8	14.5	14.7	14.3

* Calculated (on the average) from 10 egg-pods which had yielded a hatch.

(d) *Fertility.*

The best method of judging the standard of fertility is to take the average number of hoppers which hatch per egg-pod. Comparing the results in Tables I and III, the average hatch for parthenogenetically produced egg-pods was approximately one-third of the hatch for sexually produced egg-pods; i.e. 10 hoppers per egg-pod as against 33 hoppers, but although only 25 per cent. of the eggs hatched, approximately 90 per cent. of the eggs examined during the first five or six days of incubation had started to develop. Also it was thought that it was around the sixth day of incubation (at 90° F.) that development

TABLE IV.—Comparison of mated and unmated F_4 parthenogenetic generation of *Schistocerca gregaria* with ordinary stock adults (sexually produced) kept at a constant temperature of 90° F. and at a relative humidity of 60–70 per cent.

	F_4 Mated.	F_4 Unmated.	Stock adults. (Control).
Number of males	5	0	6
Number of females	5	10	10
Length of adult life of females (in days) } Average	69.2	136.4	68.3
} Minimum	40	100	36
} Maximum	95	166	108
First egg-pod (in days)	23	41	21
Last egg-pod (in days)	76	144	107
Average egg-pods per female	2.6	2.9	4.6
Average days per egg-pod	26.7	37.6	14.8
Average eggs per egg-pod	40.5	42.5	40.0
Average number of hoppers which hatched per egg-pod	34.0	10.2	33.1
Percentage of eggs which hatched	83.9	23.8	80.4
Average incubation period (in days)	13.5	14.7	14.7

stopped, because a difference in the consistency of the yolk of some eggs could be observed, and these embryos did not show active cell division.

(e) *Metabolic Rate.*

The metabolic rate of adults has already been mentioned when dealing with the length of adult life, but additional evidence in support of a reduction in the metabolic rate of females reproducing parthenogenetically is obtained when the rate of production of egg-pods (i.e. the number of days required by a female to produce an egg-pod calculated over the entire life of the female) is considered. For females reproducing parthenogenetically the average days per egg-pod ranged from 33.7 to 46.1 (Tables I and III) with one exception of 70 days. Even if this exception is excluded the average is 38.1 days, which is very much longer than the average of 20.4 days for females reproducing sexually. Also, as the result of this slowing down of the rate of oviposition, the females retained their fertility much longer, so that they may lay their last egg-pod any time up to 320 days after reaching the adult stage as against 107 days when reproducing sexually.

4. HOPPERS.

(a) *Development.*

As in the case of the rate of incubation of the eggs (Tables I and III), there is no significant difference (Table II) between the rate of development of parthenogenetically and sexually produced hoppers, but there is considerable difference in the percentage of hoppers which reach the adult stage; 34.7 per cent. of the parthenogenetically produced hoppers as compared with 52.2 per cent. of the sexually produced hoppers. This increase in mortality seemed to occur during the first instar.

(b) *Sex of Progeny.*

An important result revealed by Table II is the ratio of males to females. Without exception all parthenogenetically produced hoppers were females, whereas the ratio of males to females was 56 to 65 for sexually produced hoppers (controls). Also in the case of parthenogenetically produced females mated with ordinary stock males the progeny was of both sexes, but there was a slightly higher proportion of males (17) to females (16). The F_1 generation, from this crossing of parthenogenetically produced females with ordinary males, when allowed to interbreed gave progeny with a ratio of 14 males to 17 females. Thus judging from breeding experiments it would seem that parthenogenetically produced females and their progeny have the diploid number of chromosomes.

5. SUCCESSIVE GENERATIONS PRODUCED PARTHENOGENETICALLY.

Up to the time of writing it has been possible to produce six generations parthenogenetically. Details of five generations are given in Table III, where it can be seen that the length of hopper life varies very little and where it does, e.g., F_4 and F_5 , the shorter the hopper life the longer the time required by the adults to reach sexual maturation.

The length of adult life shows some variation over the generations. Starting with the parental stock which was produced sexually but reproduced parthenogenetically, they lived, on the average, 182.1 days. Then there was a reduction to 130.5 days for the F_1 , and to 91.4 days for F_2 , which suggested that there was a gradual reduction in the length of adult life in successive generations, but this hypothesis proved incorrect as the F_3 generation lived, on the average, 161.1 days. The F_4 and F_5 generations lived 136.4 and 107.1 days respectively. Of all these figures even the lowest gives a much longer adult life than in the case of adults reproducing sexually. If the average for the six generations is taken it gives an average length of adult life two to three times greater than that of the controls. Continuing the comparison between the successive generations reproducing parthenogenetically the rate of sexual maturation (28–41 days), the average time required to produce an egg-pod (34–40 days with one exception of 70), the average egg-pods per female (2.3–5.4), the average eggs per egg-pod (40.1–47.0), the incubation period (14.2–14.8 days), and the percentage hatch per egg-pod (23.6–28.0 hoppers), all show variations but are, on the whole, sufficiently constant to be within experimental variations. Some of these results are very similar to those for sexual reproduction, but others (see above) show a significant difference which is constant for all successive generations.

6. MATING OF PARTHENOGENETICALLY PRODUCED FEMALES WITH STOCK MALES.

Parthenogenetically produced females when kept with males copulate normally. In Table IV a comparison is made between F_4 parthenogenetically produced females breeding parthenogenetically and mated with ordinary stock males. Also a comparison is made with ordinary stock adults (controls) reproducing sexually. The F_4 females when mated lived approximately half the time (69.2 days) of those reproducing parthenogenetically (136.4 days). Thus the average length of life of parthenogenetically produced females repro-

ducing sexually is reduced to approximately the same length as that of the ordinary stock (68.3 days) reproducing sexually. Also the time required to reach sexual maturation (23 days), the average time required to produce an egg-pod (26.7 days), the percentage hatch per egg-pod (83.9), and the sex ratio have all returned to the same as that for ordinary stock locusts reproducing sexually.

7. CHROMOSOME NUMBERS.

Judging by the behaviour and the sex ratio of their progeny when mated, there is no doubt that parthenogenetically produced females have the diploid number (24) of chromosomes in their sex cells. Chromosome counts of cells from developing eggs after three to six days' incubation at 90° F. showed considerable variation. In parthenogenetically produced eggs it was found that some of the cells of the squashed preparations had the diploid number (24) of chromosomes (fig. 1) and some had the haploid number (12) for females (fig. 2) of this species. Also there appeared to be some cells with a sub-diploid number, i.e., less than 24 but more than 12, and some with supernumerary chromosomes, i.e., more than 24.

Eggs which had been produced sexually were examined and it was also found that in these preparations not all the cells contained the diploid number of chromosomes; some had the diploid number, while others had a sub-diploid number. This sub-diploid number did not seem to be constant in either the parthenogenetically or sexually produced specimens nor indeed did it seem to be constant in any one individual. As the chromosome counts and photographs were made from squash preparations it is impossible to say whether all the cells were true embryonic cells or if some were extra-embryonic cells which take no part in the formation of the hopper. Judging from the position and number of the sub-diploid cells in both sexually and parthenogenetically produced specimens it seemed that some, at least, belonged to the embryo.

8. DISCUSSION.

The fact that I have obtained locusts parthenogenetically, without any special treatment, from four random samples (10 females in each) of *Schistocerca gregaria* (three recorded in Table I, the fourth in progress at present,) and have been able to rear this species parthenogenetically for six successive generations (Table III) suggests that reproduction could occur and continue for an indefinite period by this method. This 100 per cent. success in obtaining progeny parthenogenetically from random samples of ordinary stock females is higher than was found by Norris (1954) who discontinued her experiments after the females had reached sexual maturity. Like Hamilton (1953) and Norris (1954) I have found that all progeny were females, whereas Husain and Mathur (1945) claim to have obtained this species parthenogenetically with a 50-50 ratio of males and females. Judging from the sex of the vast majority of Acrididae (see Introduction) produced parthenogenetically it would seem that Husain and Mathur's claim is not justified. So far as I know, parthenogenesis has not been observed in the field, but the lack of this evidence is not sufficient reason to say that it never occurs. As parthenogenetically produced locusts are similar in appearance to those produced sexually, the only possible way of obtaining

evidence in the field would be to collect, in a suspected area where this species is found as *solitaria*, egg-pods or emerging hoppers and isolate them until the hoppers were large enough to be sexed. If they proved to be all females then it could be assumed that they had been produced parthenogenetically. Should parthenogenesis occur, it is not likely to continue for many generations in the field, as very short flights by parthenogenetically produced females would bring them into contact with *solitaria* males in the neighbourhood. The chief advantage of parthenogenesis in the field would be to maintain a population with a high proportion of females.

In my experiments the average time required to reach sexual maturity by females reproducing parthenogenetically (Tables I and III) was 33 days at 90° F. (32.2° C.). This agrees fairly well with the 38 and 34 days which Norris (1952) found for isolated pairs, but it is a very much slower rate of sexual maturation than I found for my semi-crowded controls (21–22 days) reproducing sexually, or that recorded by Hamilton (1950) and Norris (1952) for crowded males and females. Norris (1954) says that the slower rate of sexual maturation of isolated pairs when compared with crowded locusts, is due to later maturation of some of the males, but according to my results it would seem that the rate of maturation of females plays a part, as my virgin females matured at approximately the same time as her isolated pairs.

Notwithstanding the fact that females reproducing parthenogenetically required the same time to reach sexual maturation as isolated pairs (Norris, 1952), it is interesting to note that their rate of oviposition was very much slower. Norris, who calculated the rate of oviposition as the average time between successive egg-pods, found that for isolated pairs it was 7.07 days. If I convert my results (which were calculated from the date of emergence of the adults) to the same basis as Norris's, then the average rate of oviposition for my females reproducing parthenogenetically is one egg-pod per female every 34.3 days. This is also very much slower than the rate which I found for semi-crowded controls (10.9) and Norris found under crowded conditions (7.28). Thus copulation between successive egg layings acts as a stimulus to oviposition, so that isolated pairs (which had approximately the same rate of sexual maturation as females reproducing parthenogenetically) had a much faster rate of oviposition (approximately the same as that for crowded locusts), than those reproducing parthenogenetically. Husain and Baweja (1936) say that the act of copulation by "desexualised" males stimulates the females to oviposit, and suggest that it is the mere act of copulation without the transference of any sperms. It is true Husain and Baweja removed the testes from their "desexualised" males, and therefore no sperms would be transferred, but according to their description they only removed the testes, therefore secretions from the accessory glands could be transferred during copulation, and I think that these would be sufficient to stimulate the females to oviposit, as Norris (1954) states "Readiness to copulate is associated with the presence of secretion in the accessory sexual glands, but not necessarily with the presence of spermatozoa in the receptaculum seminis". In spite of this reduction in the rate of oviposition, the total number of egg-pods per female reproducing parthenogenetically was as high as for females reproducing sexually because the former lived three times as long as the latter; this suggests that there is a difference in the metabolic rate of adults, depending on the type of reproduction. In my experiments using

parental stock locusts (Table I) the average number of egg-pods per female reproducing parthenogenetically was 5.4, but in the experiments using successive generations reproducing parthenogenetically it was 3.6 (Table III). These figures approximate to those for my controls reproducing sexually (average 4.1), and if an average of all my results for parthenogenetically produced egg-pods is taken it agrees with the average (5) given by Norris (1952) for isolated pairs. Likewise, the number of eggs per egg-pod agrees so well that it can be concluded that the fecundity of the females is the same, irrespective of the method of reproduction.

When the number of hoppers hatching per egg-pod is considered (Tables I and III), there is a marked drop in the fertility, as the average hatch per egg-pod for parthenogenetically produced eggs is less than a third (average 10 hoppers) of the figure (average 34 hoppers) for sexually produced eggs. My figure for the hoppers per egg-pod is double that found by Norris (5 per egg-pod) for her parthenogenetically produced egg-pods.

The rate of development of parthenogenetically produced eggs and hoppers (Table II) was very similar to that for sexually produced eggs and hoppers, thus the reduced "metabolic" rate of the parents had no effect on the metabolic rate of their eggs and hoppers. Also it should be noted that the rate of sexual maturation of parthenogenetically produced females, when mated, returns to the same as that for ordinary females reproducing sexually, and that the fertility of their eggs was the same as those produced sexually by ordinary stock locusts.

The really important difference between parthenogenetically and sexually produced hoppers is the fact that the former are all females. This raises the question of the number of chromosomes in the cells of these females. According to Csik and Koller (1939) and McClung (1939) the diploid number of chromosomes for this species is 23 for males and 24 for females. In my squash preparations of developing parthenogenetically produced embryos I found cells with diploid (fig. 1), sub-diploid, haploid (fig. 2) and supernumerary numbers of chromosomes, but in the sexually produced embryos I found only diploid and sub-diploid, never true haploid. The fact that sub-diploid cells were found in sexually produced embryos as well as in parthenogenetically produced ones is interesting, but a detailed examination of this subject is outside the scope of this paper. However, I should add that Green (1953) working on tadpoles and Sachs (1953) working on mammals found that cells with the sub-diploid number of chromosomes were quite common, while Rothfels (1950), Sharman (1952), White (1949) and Rees and Jamieson (1954), all working on Orthopterous insects, record cells with supernumerary chromosomes.

The presence of cells with the haploid number of chromosomes in parthenogenetically produced embryos, indicates, I think, that reduction division has occurred. Slifer and King (1932), King and Slifer (1934), Creighton (1938) and Chopard (1948) who also found haploid cells, and McNabb (1928), who says that all parthenogenetically produced females are homozygous for all characters carried, add further support to this belief.

The next problem is that of the doubling of the number of chromosomes to restore the typical diploid number in parthenogenetically produced females. As I found cells in developing embryos with the haploid number I believe meiosis is complete and that the doubling does not necessarily occur at the single cell stage but that it is a gradual process. This suggestion is supported by the

fact that I found that approximately 90 per cent. of the eggs had started to develop but only approximately 25 per cent. hatched, the others dying after the sixth or seventh day of incubation. This low percentage hatch in parthenogenetically produced eggs is due, I think, to the fact that only those embryos which succeed in restoring the diploid (and its variations of sub-diploid, etc.) number, survive and hatch. This view is shared by Slifer and King (1932) and King and Slifer (1934) working on grasshoppers, but is contrary to the views of McNabb (1928), also working on Acrididae, and Robertson (1930) working on Tetrigidae, who believe that if the egg is not penetrated by a sperm the second meiotic division is abortive and that the last polar body fuses with the ovum and restores the diploid number. Whichever of the above views proves to be correct, there can be no doubt, as shown by my experiments (Table IV), that the females produced parthenogenetically have the diploid number of chromosomes in their sex cells.

So far very little work has been done to determine the factor or factors which cause parthenogenetically produced eggs to start developing under natural conditions. Roonwal (1936) believes that in fertilised eggs of *Locusta migratoria migratorioides* the first and second cleavage division occur during the first $5\frac{1}{2}$ hours after egg-laying. This leads me to suggest that the stimulus to start cell division in parthenogenetically produced eggs is provided by oviposition.

9. SUMMARY.

1. *Schistocerca gregaria* reproduced parthenogenetically under constant and alternating conditions of temperature.
2. Six successive generations were reared parthenogenetically.
3. All the progeny were females.
4. The rate of sexual maturation was much slower than for locusts breeding sexually.
5. The average rate of oviposition was also very much slower, therefore implying that copulation stimulates the females to oviposit.
6. The average length of adult life was about three times that of females reproducing sexually.
7. The average number of egg-pods per female and the average number of eggs per egg-pod were the same as when sexually produced, but the average hatch per egg-pod was only one-third.
8. The average rate of hopper development was the same as for sexually produced hoppers.
9. Parthenogenetically produced embryos had cells with diploid, sub-diploid, haploid and supernumerary numbers of chromosomes, while sexually produced ones had only diploid and sub-diploid numbers.
10. Meiosis was complete.
11. The restoration to the diploid number of chromosomes occurred during embryonic development.
12. When parthenogenetically produced females were mated their rates of sexual maturation, oviposition, etc., were similar to those for ordinary stock locusts and their progeny gave a sex ratio of approximately 50-50 males and females.

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BOOK NOTICE.

The Physiology of Diapause in Arthropods. By A. D. LEES. Cambridge Monographs in Experimental Biology. 4. 8vo. Cambridge (C.U.P.). 1955. Pp. x + 151, text illust. Price 12s. 6d.

Much experimental analysis of the phenomenon of diapause in hibernating insects and mites has been carried out, particularly during the last fifteen years, and the results achieved in their different spheres by the physiologist, biochemist, and ecologist have been integrated and assessed in this study.

A very full bibliography provides a comprehensive guide to the literature of this field.

THE LARVAL STAGES OF *COENAGRION MERCURIALE* (CHARP.) (ODONATA: COENAGRIIDAE).

By PHILIP S. CORBET, Ph.D., F.R.E.S.

(Department of Zoology, University of Cambridge.)

INTRODUCTION.

SEVERAL descriptions exist of the larva of *C. mercuriale* (see especially Lucas, 1930), but these refer only to the final instar. Perhaps the two most important reasons for describing the early instars are to provide data for comparative ontogenetic studies and to make possible the identification of small larvae in the field. Accordingly, it is the purpose of this paper to describe some of the principal morphological changes occurring during development and to show the extent of the variation liable to be encountered in the last two larval instars. In addition, attention is drawn to characters which have been found reliable for identification of field material.

MATERIAL AND METHODS.

The reared larvae used as a basis for description were derived from a batch of eggs collected by Lt.-Col. F. C. Fraser from the River Oberwater, in the New Forest, Hampshire, on 1st July, 1951. These eggs had been laid in a stem of *Alisma plantago-aquatica* L., a plant which is common along the margins of this stream. The stem containing the eggs was received by the writer on 9th July, and was kept in shade in a north-facing room until 20th July. From 20th July onwards the eggs were kept at a room temperature of about 18–20° C., being well illuminated from a large window facing east.

Close inspection of the eggs was not possible during hatching, which began soon after 20th July and probably continued for about three weeks. After 4th August, instar 2 larvae were isolated from the stock dish containing the eggs, and were reared each in a separate container. On 6th August, eleven larvae under inspection were distributed as follows: instar 3 (1); instar 4 (8); instar 5 (2). On 9th October, the distribution of the four larvae remaining was: instar 4 (1); instar 6 (1); instar 7 (2). Only one larva survived instar 7, and this entered subsequent instars as follows: 8 (25th October); 9 (8th November); 10 (22nd November); 11 (10th December); 12 (15th January); 13 (25th February). Instar 13 was the final larval stage from which a male imago emerged on 13th April, 1952. Descriptions of instars 2 to 11, inclusive, are based entirely on reared material. Larvae collected from Hampshire and Glamorganshire provide supplementary data for the penultimate and final instars. There is no reason to suppose that the number of larval instars is invariably thirteen.

Measurements were made upon living material, but exuviae were used for descriptions of the antennae, labium and tarsi in reared specimens. The body-lengths given represent the distance from the anterior margin of the head to the posterior margin of abdominal segment 10. The caudal lamellae are

excluded from this measurement since, in the field, where such values have principal application, these structures are frequently either missing or partly regenerated.

Throughout its growth the larva reared to maturity was kept in a centrally-heated room. In the early instars, Protozoa and Cladocera were provided as food; from instar 7 onwards, the larva fed entirely on small Oligochaeta (Enchytraeidae).

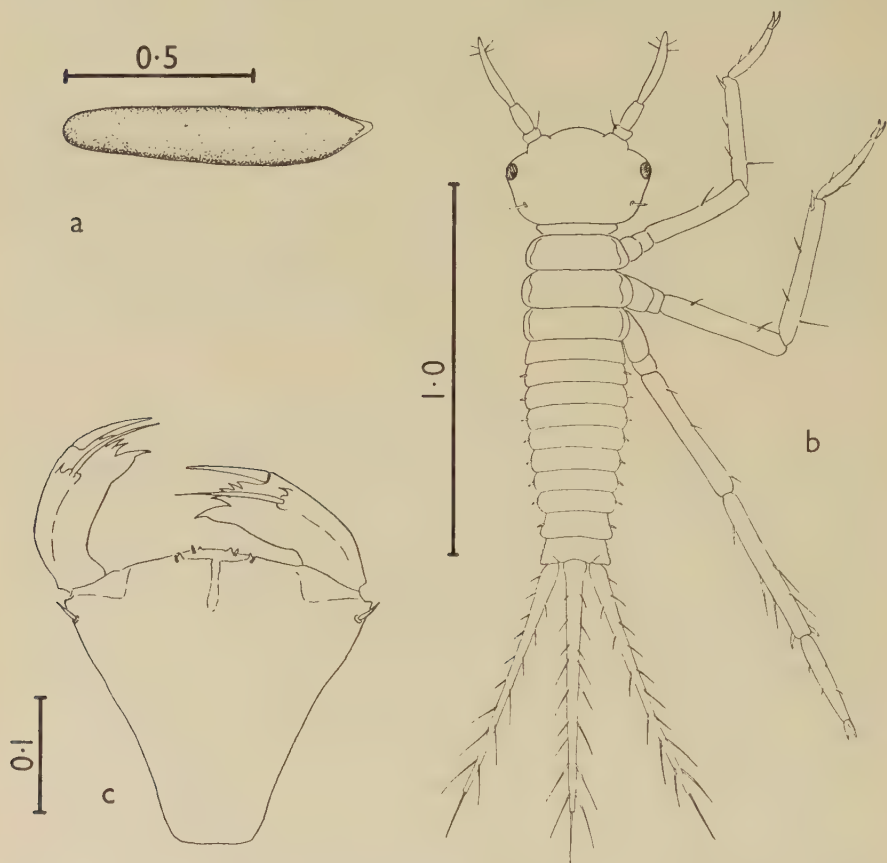


FIG. 1.—a. Egg. b. Instar 2 larva. c. Labium of instar 2. Measurements are given in millimetres, and read from the bottom upwards.

It is worthy of mention that, after metamorphosis has been completed, it is probable that emergence can be postponed for a considerable time. Thus, in the specimen that emerged on 13th April, 1952, the tissues of the labium had been lying retracted within the postmentum since 22nd March. It appears that in most Odonata this condition is reached about two or three days before emergence. In an attempt to precipitate the emergence of the reared specimen, the dish containing the larva was placed in direct sunlight at about 10 a.m. on 13th April. The water temperature rose rapidly to about 30°, and emergence

TABLE I.—Summary of characters of reared larvae.

	Instar.												
I	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	
Antennal segments	3	4 (8)	5 (3)	5 (4)	5 (6)	6 (2)	6	6	6	6	6	7	
Premental setae	.	(7)	1 + 1 (3)	1 + 1 (3) 2 + 1	2 + 2 (3) 2 + 1 1 + 1	2 + 2 (2)	2 + 1 2	2 1 + 3	2 1 + 3	3 + 3	3 + 3	3 1 + 3	
Palpal setae	1 & 1	2 & 2 (6) 2 & 1	2 & 2 (3)	2 & 2 (4)	2 & 2 (5)	2 & 2 (2)	3 & 3	3 & 3	4 & 3	4 & 4	4 & 4	5 & 5	
Tarsal segments	1	1 (8)	2 (3)	2 (4)	2 (6)	3 (2)	3	3	3	3	3	3	
Abdominal segments covered by wing-sheaths	.	.	.	.	.	.	.	$\frac{1}{2}$	1	1 $\frac{1}{2}$	2 $\frac{1}{2}$	4	
Anal cerci	.	.	.	.	.	.	×	×	×	×	×	×	
Head-width (mm.)	0.40	0.48	0.61	0.73	0.89	1.10	1.30	1.63	1.90	2.30	2.80	3.25	
Length of caudal lamellae (mm.)	0.8	0.9	1.1	1.3	1.5	1.6	1.9	2.3	2.4	2.5	3.4	3.6	
Body-length (mm.)	1.2	1.4	1.6	1.9	2.2	2.9	3.8	5.5	6.8	8.4	11.3	12.5	

Note.—When the frequency of an observation exceeds one, it has been recorded in parentheses.

followed within three hours. This ability to postpone emergence for a considerable period until conditions become favourable might well be of adaptive significance. Not only would it ensure that transformation occurred under optimal conditions, but it would also tend to synchronise the appearance of the adult stage.

DEVELOPMENT.

The first larval instar (the pronymph) was not observed. Instar 2 is shown in fig. 1*b* and the final (13th) instar in fig. 4. The external morphological changes associated with this development are described below under the appropriate headings. The principal characters of the reared series are itemised in Table I; those of the penultimate and final instars (field material) appear in Table II.

TABLE II.—*Summary of characters of larvae obtained from Hampshire and Glamorganshire.*

	Instar.	
	Penultimate.	Final.
Antennal segments . . .	6 (25)	7 (6); 6 (4); 7 6 (1)
Premental setae . . .	3 + 3 (16)	3 ₁ + 13 (5)
	4 + 13 (3)	4 + 4 (2)
	3 ₁ + 13 (2)	4 + 13 (1)
	3 ₁ + 3 (2)	3 ₁ + 3 (1)
	3 + 12 (2)	3 + 3 (1)
		3 + 2 (1)*
Palpal setae . . .	5 & 5 (9)	5 & 5 (9)
	4 & 4 (7)	6 & 5 (1)
	5 & 4 (6)	7 & 6 (1)*
	5 & 14 (2)	
	4 ₁ & 4 (1)	

Note.—In cases of asymmetry, no account has been taken of whether the excess was to the right or to the left. The higher value has always been written first. The figures in parentheses give the frequencies.

* This specimen possessed a slightly deformed right palpus. Furthermore, it came from a small, isolated colony in which variation may have been unusually wide. It is doubtful therefore whether it can be considered typical of the species.

Antennae.

As is probably the case in all Odonata (see Gardner, 1951), the antenna of instar 2 consists of three segments only: scape, pedicel and distale. Until the six-segmented condition is reached, additional segments arise by division of the proximal segment of the flagellum (the segments derived from the distale of instar 2); neither scape nor pedicel divides. From instar 7 onwards, the number of segments remains stable at six until the final instar when, in rather more than half of the specimens, the apical segment of the flagellum undergoes division. This ultimate division is, at the best, poorly delimited, high magnification and

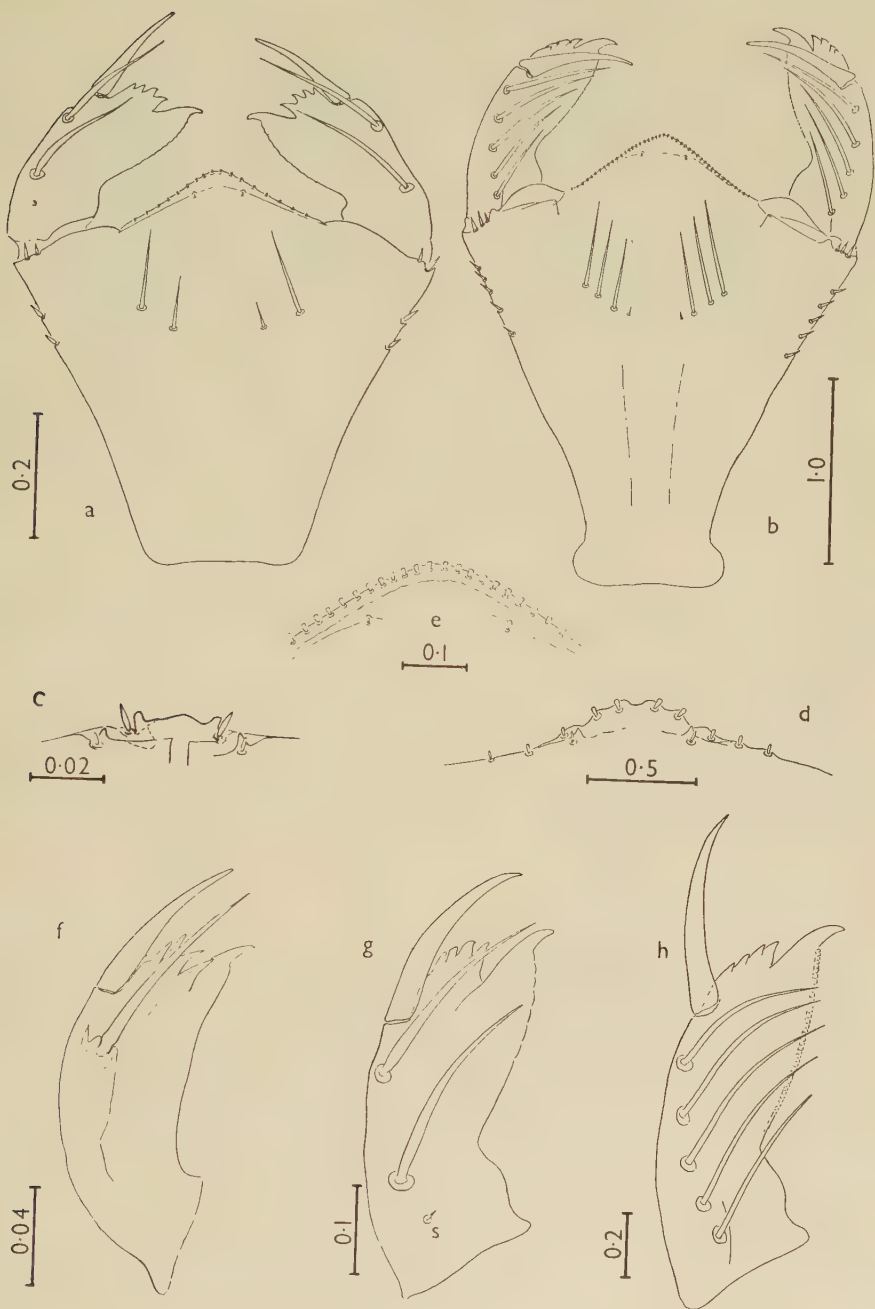


FIG. 2.—*a, b*. Labium. *c-e*. Distal margin of median lobe. *f-h*. Left labial palpus. *a*, instar 6; *b*, instar 13; *c*, instar 2; *d*, instar 3; *e*, instar 13; *f*, instar 2; *g*, instar 7; *h*, instar 13. (*s*: setella.) Measurements are given in millimetres and, when not horizontal, read from the bottom upwards.

careful disposition of lighting being required to discern it. Lucas (1930) describes the antenna as being seven-segmented and, in this respect, is followed by Fraser (1949). Inspection of a wider range of material, however, has shown this character not to be trenchant. It is probable that the antenna is always six-segmented in the penultimate instar. It consists of three segments in the imago.

A small, lateral, delicate spine is present on the apical segment of all instars (fig. 5c) excepting that of the final instar in the seven-segmented condition. In the latter case the spine is borne on the penultimate segment, immediately proximal to the last division (fig. 5d). A similar structure has been described in other species of *Coenagrion* (Balfour-Browne, 1909, and Gardner, 1954a).

Labium.

The labium remains of the same general shape throughout development (see figs. 1c, 2a and 2b) but changes occur in the number and disposition of setae and spines. Terms used to describe parts of the labium are those defined by Corbet (1953).

Prementum.

There is an increase in the number of spiniform setae on the lateral margin, from one in instar 2 to about five in instar 13. One spiniform seta appears also at the insertion of the palpus in instar 3, and this number has usually increased to three by the final instar.

The primary premental seta arises in instar 4. Usually, two more setae are added during development, the normal complement of the final instar being three on each side. Variation in the degree of development of the mesial precursors is considerable, but it is safe to assume either three or four setae in both penultimate and final instars. All setae are added mesially.

Median Lobe.

Two pairs of very small spines are situated near the middle of the distal margin in instar 2. Associated with each spine is a seta (fig. 2c). Those of the lateral pair of spines lie slightly posterior to those of the mesial pair. Similar structures have been discerned in most other instar 2 larvae inspected at sufficient magnification, and it has been suggested that they represent vestigial lobes of the ligula (see Corbet, 1953). In *C. mercuriale* the antero-mesial setae appear to be the forerunners of the series of claviform setae developing later on the distal margin. The postero-lateral setae remain inconspicuous, and come to lie progressively further from the distal margin. They are still visible in the final instar.

The claviform setae on the distal margin increase with each ecdysis, and come to number about forty-five in the final instar.

The median lobes of instars 2, 3 and 13 are illustrated in figs. 2c, 2d and 2e.

Palpus.

The palpus of instar 2 (fig. 2f) is typical of the Odonata in possessing a single palpal seta and coarse dentations on the distal margin. An interesting feature is a small spine immediately lateral to the insertion of the palpal seta. This

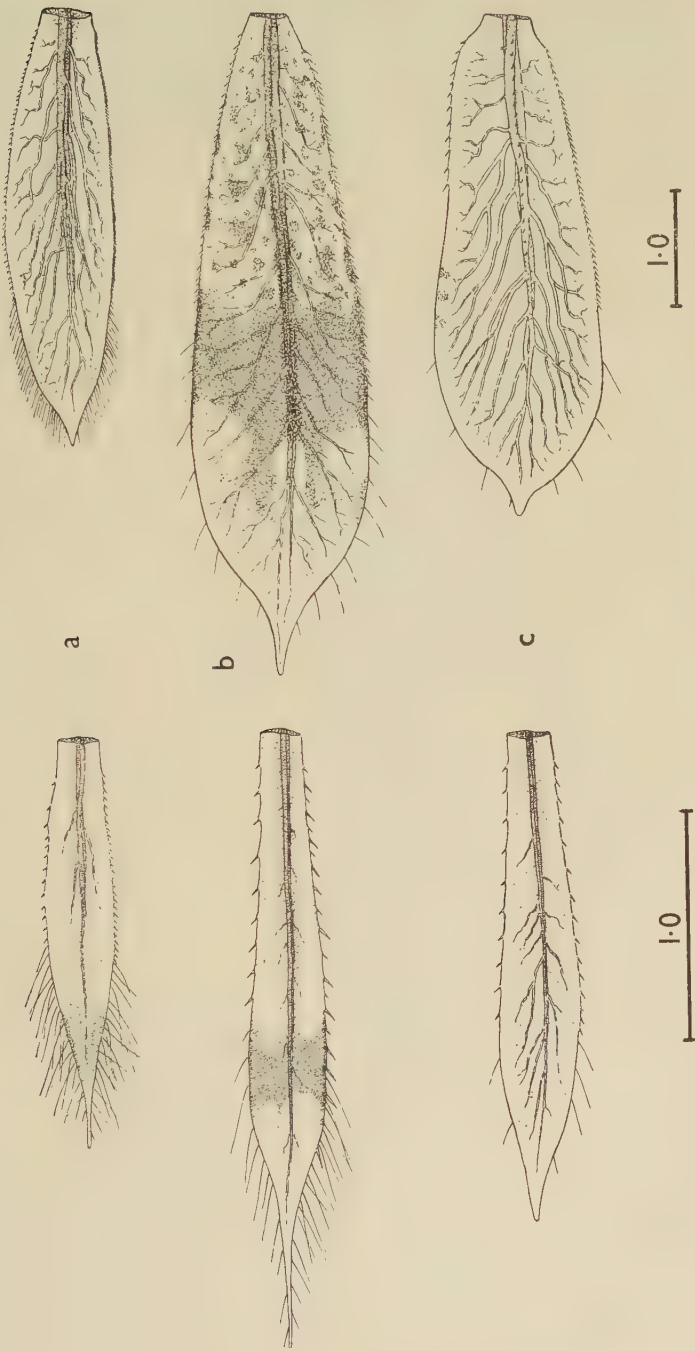


FIG. 3.—Caudal lamellae of three species of Coenagriidae : left, in approximately the seventh instar (body-length 3.5 mm.) ; right, in the final instar. a, *C. mercuriale* ; b, *P. nymphula* ; c, *C. tenellum*.

structure seems to have been noticed first in *Enallagma hageni* (Walsh) and *E. signatum* (Hagen) by Wilson (1920), and has since been found in *Coenagrion hastulatum* (Charp.) (Gardner, 1954a) and in *Enallagma cyathigerum* (Charp.) (Gardner, 1954b). It requires high magnification to be discerned in *C. mercuriale* but may well prove a useful character for distinguishing this species from certain others in early instars. This spine persists as a definite structure until instar 5; it is barely visible in instar 6, and has disappeared in instar 7 (see fig. 2g).

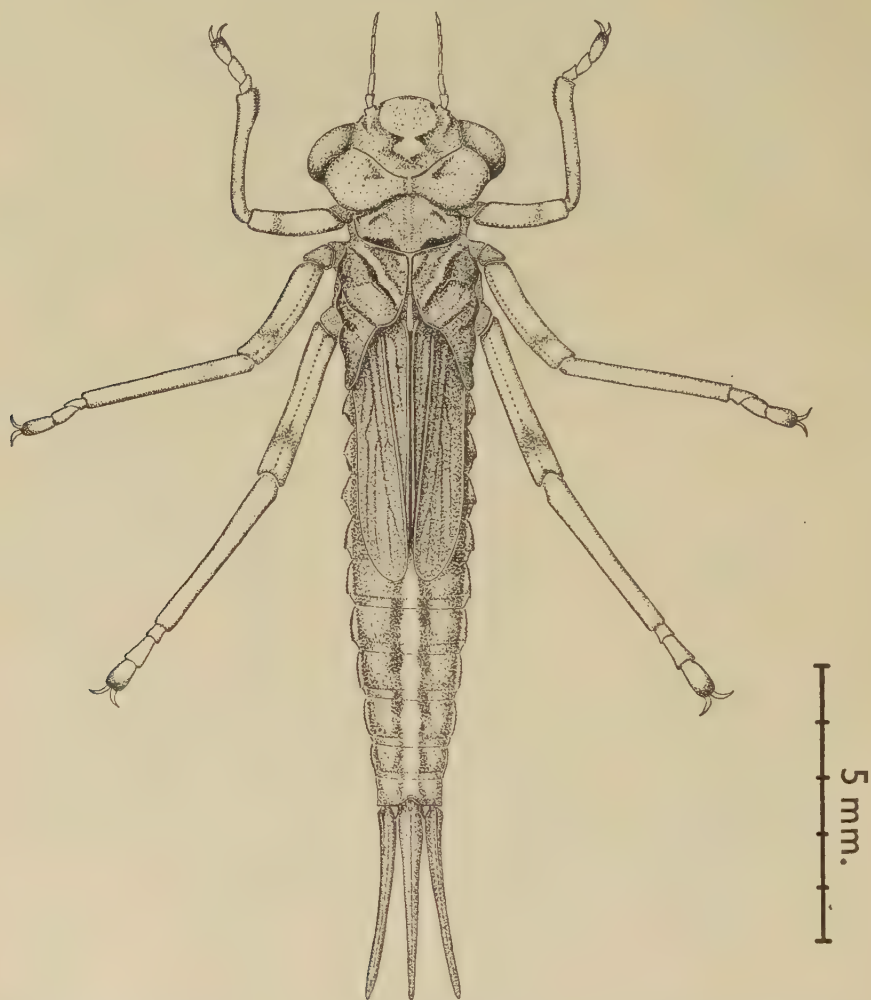


FIG. 4.—Final instar larva. A female collected from the River Oberwater, Hampshire, in November, 1952.

During development, the four dentations on the distal margin become shallower. Serrations become visible on the inner margin in instar 3, and increase in size and number during development. The strengthening of the

margin is doubtless related to its gripping action against the claviform setae on the distal margin of the median lobe.

In all but one of the cases observed, palpal setae were added at the proximal end of the series. The exception was provided by a penultimate instar larva from Hampshire in which it appeared that two setae had been added at the last ecdysis, one by proximal addition and the other by an interpolation proximal to the distal seta. It is possible, however, that the apparent interpolation represented regeneration of a damaged seta. It seems to be the rule in *C. mercuriale* that palpal setae are only added proximally; thus, a maximum of one seta on each palpus can be added at an ecdysis. It has been suggested that addition by interpolation is associated with a need for a greater number of setae than there have been ecdyses (Corbet, 1951). If this is so, there is clearly no demand for the development of such a process in *C. mercuriale*, in which the palpal setal formula rarely exceeds 5 & 5 in the final instar.

The setella (fig. 2g) is not always well-developed prior to an addition, but is often present as a small tubercle bearing a rudimentary seta.

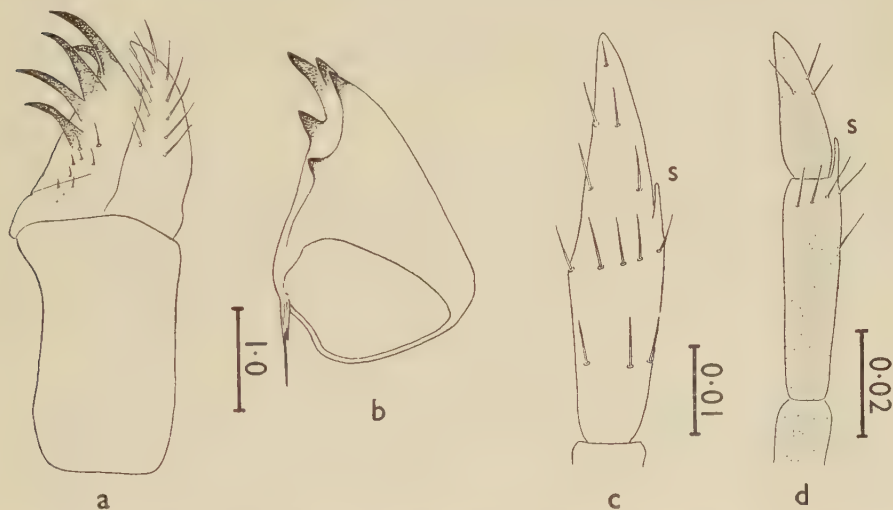


FIG. 5.—*a, b.* Mouthparts (right side) of final instar, dorsal view. *a*, Maxilla; *b*, mandible. *c, d.* Apex of antenna to show lateral spine (*s*). *c*, Instar 3; *d*, final instar. Measurements are given in millimetres, and read from the top downwards.

Caudal Lamellae.

During development the caudal lamellae change markedly in shape (figs. 1b and 3a). Initially, they are long (relative to body-length), slender and lanceolate, but, from about instar 6 onwards, become progressively shorter, broader and more spatulate. Lucas (1900) considered that, in the final instar, *C. mercuriale* could be distinguished from all other species of *Coenagrion* by the shape and size of its caudal lamellae. These probably provide the most reliable characters upon which to base a quick identification in the field, although care must be taken to avoid specimens in which regeneration is taking place. By instar 7, the shape of the lamella is sufficiently distinctive for it to be used to separate

C. mercuriale from either *Pyrrhosoma nymphula* (Sülzer) or *Ceriagrion tenellum* (Villers) (fig. 3).

The change in length of the caudal lamellae relative to that of the body is shown graphically in fig. 6. It is possible that a knowledge of this relationship for other Zygoptera might assist the identification of early instars.

Anal Cerci.

These appear first in a rudimentary form in instar 8. From instar 9 onwards they increase regularly in size.

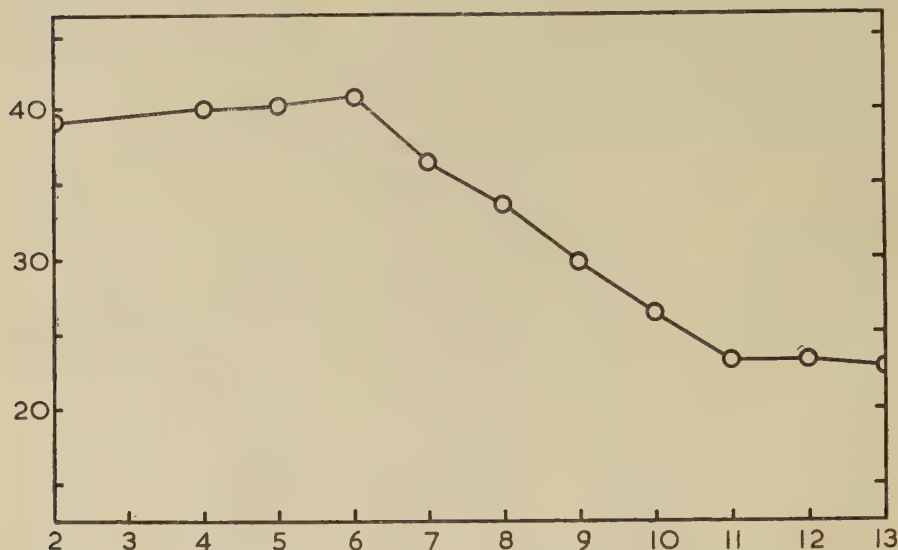


FIG. 6.—Change in length of the caudal lamellae relative to that of the body during development. *Abscissa*: instars. *Ordinate*: percentage of overall length contributed by caudal lamellae.

Wing-sheaths.

Pleural ridges on the meso- and metathorax are first visible in instar 6. Two raised points appear on the ridges in instar 7 and, from instar 8 onwards, their length increases rapidly. The number of abdominal segments covered by the wing-sheaths forms a useful character for field recognition of the last three larval instars (see Table I).

Head.

The average increase in head-width observed at each ecdysis was about 21 per cent, or a ratio of 1.209. The dorsal outline of the head undergoes marked change during development (cf. figs. 1b and 4). In later instars the head becomes antero-posteriorly shortened, and possesses a distinctive shape. The angle at the post-ocular margin is less acute than in either *P. nymphula* (Gardner and MacNeill, 1950) or *C. tenellum* (Gardner, 1954b).

IDENTIFICATION CHARACTERS.

In Britain, *C. mercuriale* occurs typically in small streams draining acid peat-bogs. Larvae usually favour the more rapidly-flowing regions and, consequently, are not likely to be found in company with any other species of *Coenagrion*. There are probably only four species of British Coenagriidae that will ever be collected with larvae of *C. mercuriale*. Two of these, *Ischnura elegans* (Van der Linden) and *I. pumilio* (Charp.), are very uncommon in peat runnels: the first, on account of its customary preference for lentic habitats, and the second, on account of its extreme rarity. The remaining two species, *P. nymphula* and *C. tenellum*, are frequently found in association with *C. mercuriale*.

From both these dragonflies, *C. mercuriale* may be distinguished by its unusually constant colour, a pale yellow-green, by its short, obtuse caudal lamellae and by its narrow head. After instar 4 (ca. 1.6 mm.), it can be separated from *P. nymphula* by the absence of dark pigment on the apical half of the caudal lamella (Gardner and MacNeill, 1950). Separation from *C. tenellum* is made possible after instar 5 (ca. 2.0 mm.) by the presence of more than one premental seta on each side of the labium.

SUMMARY.

1. *C. mercuriale* has been reared from egg to imago.
2. The principal changes in external morphology that take place during development are described.
3. Attention is drawn to characters that can be used to identify larvae from the fifth instar onwards.

ACKNOWLEDGEMENTS.

I am indebted to Lt.-Col. F. C. Fraser for obtaining the eggs from which the reared specimens were derived, to Mr. A. E. Gardner for the loan of a microscope slide used in the production of fig. 1a, and to Mr. J. Cowley for telling me of the site of a newly-discovered colony in Glamorganshire. I wish to thank Professor V. B. Wigglesworth, C.B.E., F.R.S. and Mr. A. E. Gardner for reading and criticising the typescript. I am grateful to the Department of Scientific and Industrial Research for financial assistance while this work was in progress.

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ON THE LAST INSTAR LARVA OF *TIPULA LIVIDA* VAN DER WULP (DIPTERA, TIPULIDAE) WITH NOTES ON THE FRONTO-CLYPEAL REGION OF LARVAL TIPULINAE AND CATERPILLARS.

By J. R. CHISWELL, B.Sc., F.R.E.S.

(Department of Zoology, University of Bristol.)

1. THE LAST INSTAR LARVA OF *TIPULA LIVIDA* VAN DER WULP.

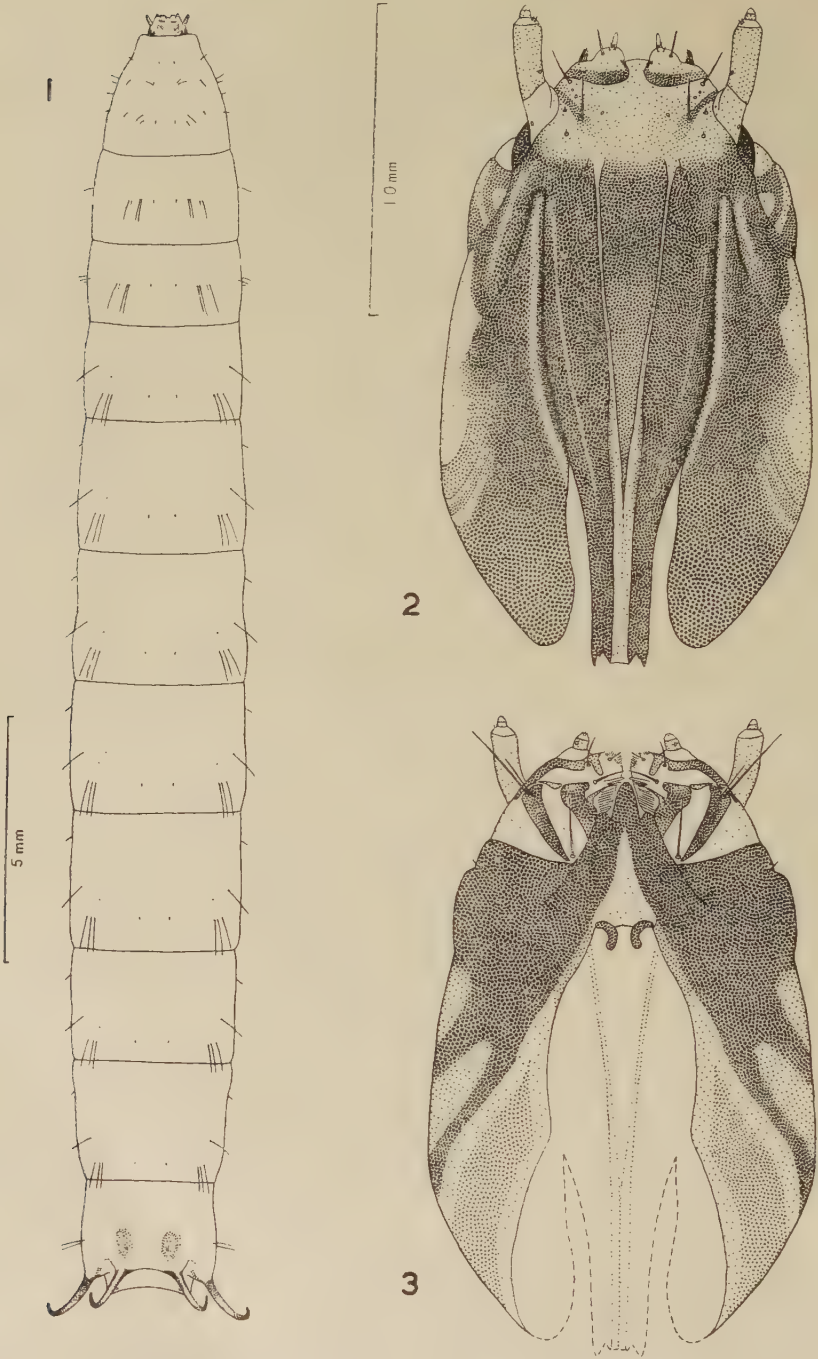
LARVAE which were later discovered to be those of *Tipula livida* van der Wulp were first found (20.ix.52) under loose, damp moss on the floor of a beechwood at Ford, nr. Castle Coombe, Wilts. Other larvae were later (spring, 1954) found on the top inch or so of moist leaf mould and soil in Leigh Woods near Bristol. *Tipula livida* is new to Britain and a note on the adult has been published elsewhere (Chiswell, 1954). Beling (1878) described a larva which is almost certainly that of *T. livida*, but which he identified as *Tipula selene* Meigen. The larvae of *T. selene* are, however, quite unlike those of *T. livida*, and cannot be confused with them.

Last instar larva.—Length 25–30 mm., breadth 3–4 mm. Cuticle unpigmented, clothed with very short adpressed pale brown silky pubescence, longest and densest on the first three or four segments.

Head capsule.—Massive, oval in dorsal or ventral view, somewhat flattened dorso-ventrally; largely dark brown or black except for extensive pale oval areas laterally; dorsal surface (fig. 2) with posterior longitudinal incisions about one-third of length of head; each incision continuous anteriorly with a broad, rather deep groove¹ that extends forward almost to dorsal articulation of mandible; the incisions and grooves separate the median fronto-clypeal region from the mussel-shaped lateral walls of the head. Fronto-clypeal region with pale cleavage lines almost straight, converging posteriorly before running parallel and close together to hind margin of head². Lateral walls of head thick and heavily sclerotised anteriorly, thinner and less heavily sclerotised behind; rather large pale oval area laterally; posterior parts with numerous fine concentric rings and intersecting radial lines of darker colour; a small, inconspicuous seta situated laterally just behind base of each maxilla and in line with its outer margin; lateral walls incomplete ventrally (fig. 3), ventral edges sinuate, meeting in the mid-line anteriorly. Hypostomal lobe heavily sclerotised, with seven rounded teeth as in fig. 11; a pale membranous, triangular area of cuticle mid-ventrally behind hypostomal lobe, posterior side of triangle with two small reniform sclerites (on which insert some of the extrinsic head capsule retractor muscles). Labrum (fig. 4) consists of a pair of lateral sclerotised lobes separated by a median area of thin, unpigmented cuticle; each lateral lobe with a small unpigmented anterior protrusion which bears three fairly large setae; innermost seta with two minute setae among a tuft of fine hairs at its base; anterior margin of lateral lobe laterad of pro-

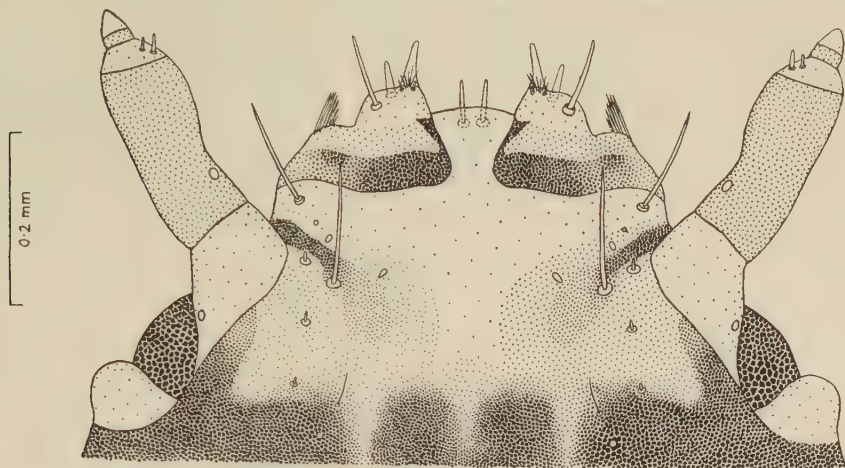
¹ Each groove marks the position of an internal strengthening ridge that extends backwards along the median side of the posterior incision to the hind margin of the head.

² The cleavage lines apparently join together just posterior to the bases of the posterior incisions to form the typical median coronal cleavage line, but this is not so. They are in fact separated by a thin, deep, internal septum which is a posterior continuation of the facial apotome and is not visible externally. The septum has a thickened and sclerotised ventral edge from which originate the posterior pharyngeal dilator muscles.

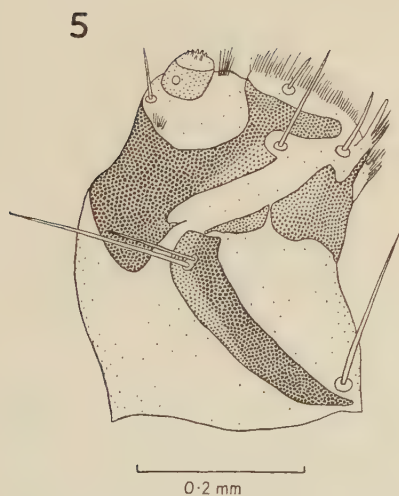


FIGS. 1-3.—(1) Entire larva ; dorsal view. (2) Head capsule ; dorsal view. (3) Same ; ventral view.

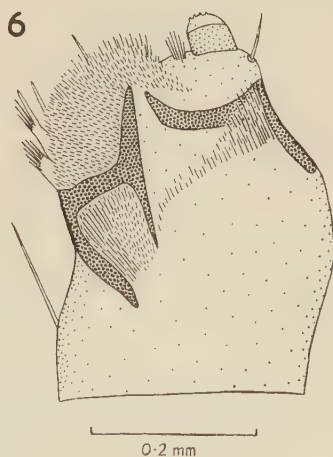
trusion with a dense tuft of rather stout hairs; ventral or epipharyngeal surface of labrum densely hairy, with a pair of setae near median anterior margin, and a pair of narrow, curved, transversely arranged tormae posteriorly; behind the tormae a transverse row of four conical, backwardly directed teeth; inner pair with apex of each truncate and bearing two very small peg-like setae. Clypeus separated from labrum by a transverse area of flexible, unpigmented cuticle; anterior part of clypeus, between antennal bases (fig. 4), lightly sclerotised and pale brown except for a pair of more heavily sclerotised, oblique lateral bands and a median unpigmented area; posterior part of clypeus heavily sclerotised, dark brown or black, divided into three parts by dorsal cleavage lines and continuous behind



4



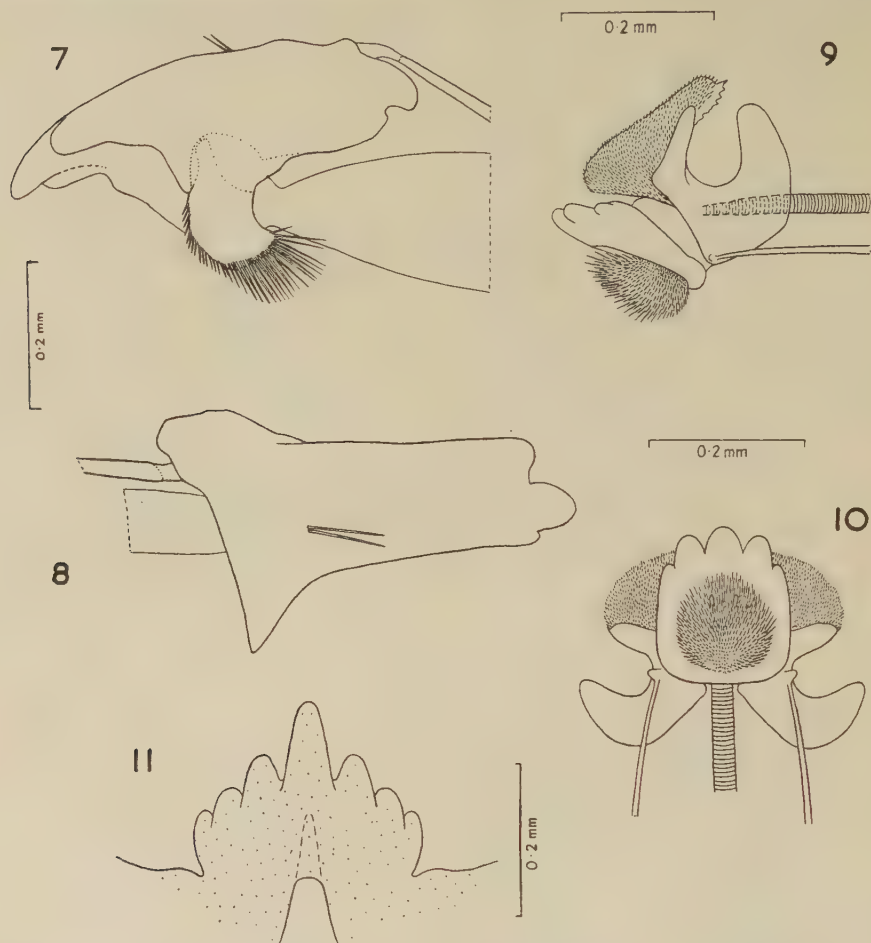
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FIGS. 4-6.—(4) Anterior part of head capsule to show antennae, labrum and anterior part of clypeus; dorsal view. (5) Right maxilla; ventral view. (6) Same, dorsal view.

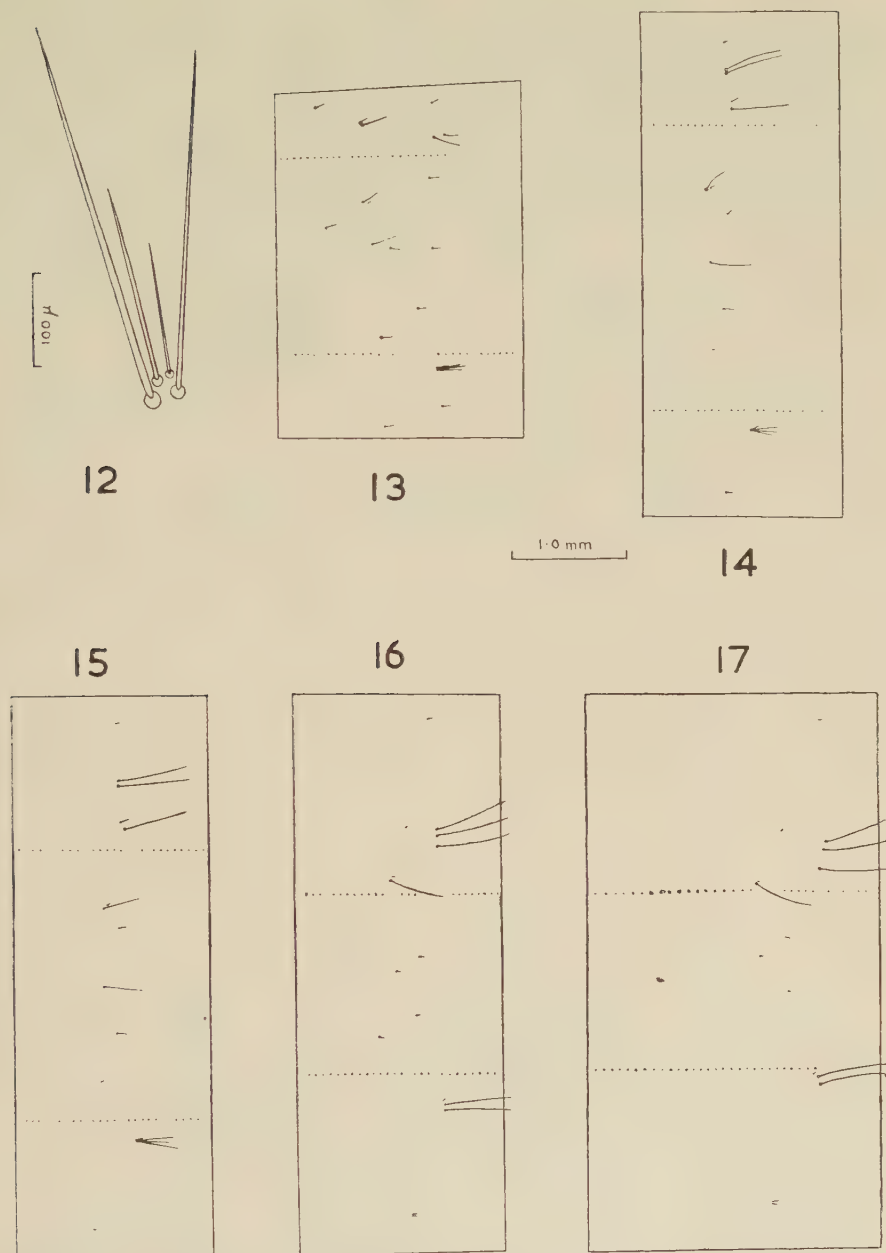
with frontal region; each side of clypeus with six setae and four small pale punctures located as in fig. 4; of these, one seta and one puncture lie on dark brown posterior part of clypeus and are difficult to see. Antenna 1 segmented, reddish-brown, cylindrical, slightly curved and constricted at middle; with a small circular sensory plate³ antero-dorsally near base, and with a similar sensory plate laterally on basal articular membrane;



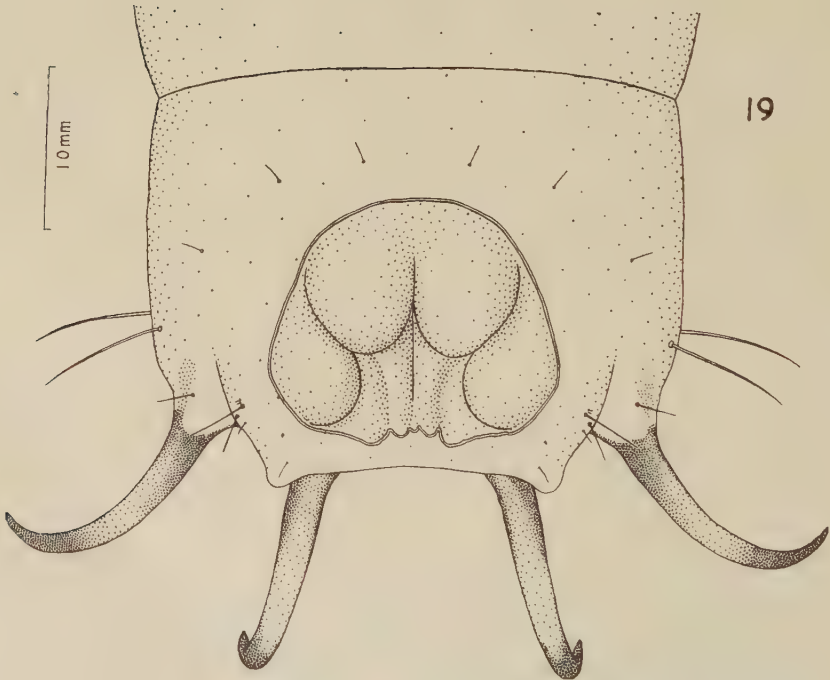
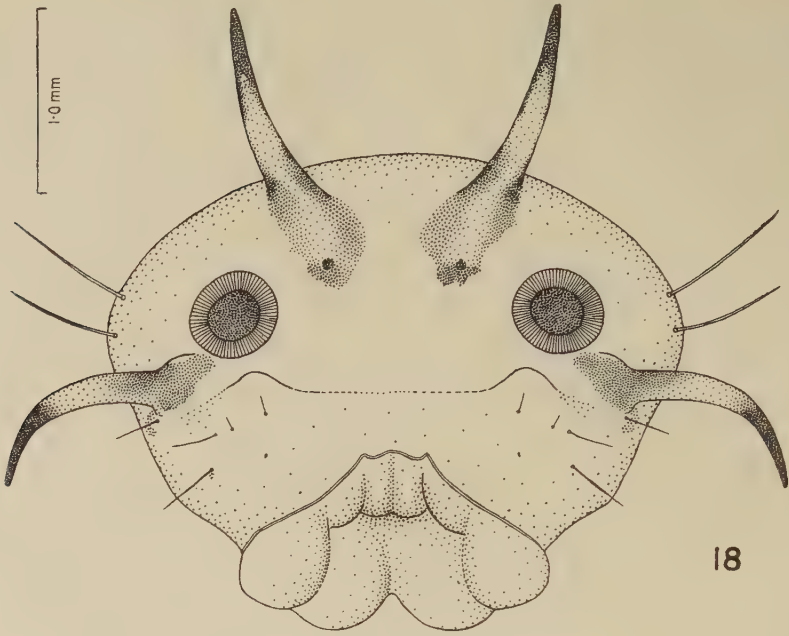
FIGS. 7-11.—(7) Right mandible, with parts of the apodemes of the adductor and abductor muscles; dorsal view. (8) Same; lateral view. (9) Hypopharynx and labium; from left side. (10) Same, ventral view. (11) Hypostomal lobe, ventral view.

apex membranous, with two minute peg-like setae antero-dorsally and an apical papilla with sclerotised base and membranous conical tip. Mandible (figs. 7 and 8) with a single sub-apical dorsal tooth and three ventral teeth, the first large, forming apex of mandible, the second smaller, and the third merely a low prominence on ventral cutting edge. Dorsal prosthecal lobe well developed, densely clothed with stout hairs on its ventral surface

³ The "auditory plate" of Alexander (1920), Wardle and Taylor (1926) and Oldham (1928).



FIGS. 12-17.—Diagrams of chaetotaxy of thoracic and first seven abdominal segments, showing left side of each segment from mid-dorsal to mid-ventral line. (12) High power drawing of group of setae on lateral part of venter of each thoracic segment. (13) Prothorax. (14) Mesothorax. (15) Metathorax. (16) First abdominal segment. (17) Abdominal segments 2-7 inclusive.



FIGS. 18-19.—(18) Last abdominal segment, showing spiracular disc and anal field; posterior view. (19) Same; ventral view.

and along its anterior and median margins. Outer (lateral) surface of mandible with two close-set setae near base (fig. 8). Maxilla: ventral surface (fig. 5) with cardo narrowly wedge-shaped, slightly curved, bearing two setae near distal end and with a single seta on membranous area near base; stipes with three distinct sclerites, two median and one distal; median sclerites extend mesad from distal end of cardo, the second and larger one extends around inner margin of maxilla on to its dorsal surface as a simple proximal arm and a T-shaped distal arm (fig. 6); distal sclerite large, extending around outer margin of maxilla on to its dorsal surface as a curved transverse tongue (fig. 6); outer apical lobe of maxilla⁴ membranous, with a rather small slender seta laterally, two small tufts of

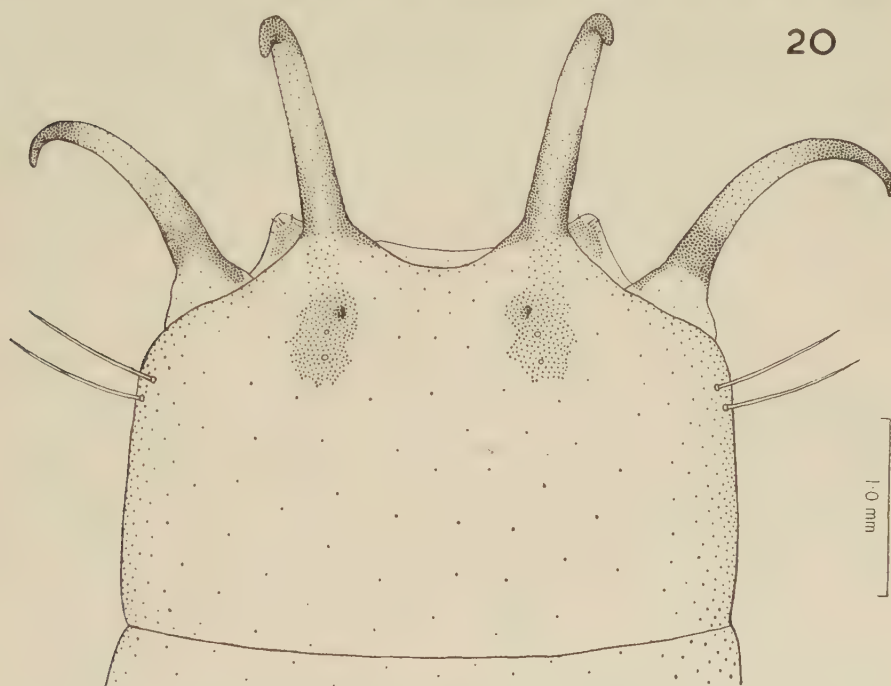


FIG. 20.—Last abdominal segment; dorsal view.

hairs, and a short, 1-segmented cylindrical palp; palp with small circular sense organ in ventro-lateral wall, and a number of minute sensory papillae on membranous apex; inner apical lobe of maxilla largely membranous, densely hairy along anterior and inner margins and on dorsal surface, ventral surface crossed by a transverse tongue of distal stipital sclerite, separating a distal (anterior) seta from two proximal (posterior) setae; inner margin of inner apical lobe with two small processes, each with dense apical tuft of stout hairs. Hypopharynx (figs. 9 and 10) membranous, densely pubescent, spoon-shaped with concave dorsal surface, supported below by a median sclerite with a pair of U-shaped lateral arms which probably represent the hypopharyngeal suspensors (Cook, 1944); base of each lateral arm with a small knob or process from which arises the apodeme of one of the paired labial retractor muscles; salivary duct opens below hypopharynx, through a hole in median part of supporting sclerite; hypopharynx with ventral membranous connection to broad area of dorsal side of labium. Labium with five teeth on anterior margin

⁴ Which represents the palpifer, according to Cook (1944).

(fig. 10), heavily sclerotised except for a ventral oval membranous area which is densely covered with stout hairs; a pair of rather short peg-like setae arises from the membrane among the hairs.

Chaetotaxy.—The setae on the head have already been described. The arrangement and relative sizes of the setae on the thoracic and first seven abdominal segments are shown diagrammatically in figs. 12–17. The setae on the eighth abdominal segment are shown in figs. 18, 19 and 20.

Spiracular disc.—Dorsal and lateral lobes of disc are heavily sclerotised, long, slender, curved horns, black at tip and base and brown between; surface of horns with minute transverse rugae. Dorsal horns curved upwards and forwards, lateral horns downwards and forwards. Dorsal horns with sclerotisation extending ventrally on to surface of spiracular disc between spiracles as a large dark brown patch; with a smaller patch at base of each lateral horn below spiracles (fig. 18). Dorsal surface of eighth segment with two large brown patches each joined to base of dorsal horn by a pale brown area (fig. 20). Ventral lobes fleshy, short and broad; each with small, brown to pale brown, crescentic or angular transverse patch just before tip; tip with six minute setae as in fig. 20. Spiracles almost circular, about three diameters apart; central scar black and plate dark brown.

Anal field.⁵—Glabrous, with marginal band brown or pale brown. Anal papillae apparently represented by four rounded lobes anterior to the anus (fig. 19).

2. THE FRONTO-CLYPEAL REGION OF LARVAL TIPULINAE AND CATERPILLARS.

Snodgrass (1947, pp. 35–37) defends the view that the area between the dorsal cleavage lines on the head of larval Diptera should be regarded as the fronto-clypeus, rather than as the frons (Anthon, 1943) or as the clypeus (Cook 1944). He furthermore maintains (p. 6 and p. 45, para. 7) that in all insects the origins of the facial muscles always lie between the dorsal cleavage lines, whereas those of the maxillary and mandibular muscles always lie outside the cleavage lines. I have found exceptions to this rule among Tipulinae. Cook (1944, fig. 14) shows that the origins of all the facial muscles in the larva of *Holorusia rubiginosa* Loew lie between the dorsal cleavage lines, and I have found the same to be true of the facial muscles of the larva of *Dictenidia bimaculata* L. In the larval heads of *Tipula paludosa* Meig. and *T. irrorata* Macq., however, the cibarial dilator muscles, the anterior pharyngeal dilator muscles, and the oral arm retractor muscles all originate outside the cleavage lines and thus do not obey Snodgrass's rule. These muscles lie mesad of the two longitudinal internal strengthening ridges of the head and it is clear, therefore, that in some *Tipula* larvae the fronto-clypeal region extends laterally beyond the cleavage lines towards the internal ridges. The facial apotome thus represents only the median part of the fronto-clypeus, a situation recognised by Snodgrass as a general possibility (p. 46, para. 14). The external sulci corresponding to the internal ridges have been used in the first part of this paper to locate the fronto-clypeal region, but it should be made clear that posteriorly the area enclosed by the ridges is not exclusively frontal, since here, between the posterior incisions of the head capsule, the median wall of each ridge bears the insertions of the most dorsal sheet of mandibular adductor muscles.

⁵ The anal field is the area bounded by a circular, narrow band of brown or black sclerotised cuticle that includes the anus and the anal papillae or anal lobes.

Hinton (1948) has already shown that Snodgrass' rule mentioned above holds for neither the Trichoptera nor Lepidoptera, pointing out that in the larvae of many of the more primitive Lepidoptera the origins of some of the mandibular adductor muscles lie between the cleavage lines, and that in all trichopterous and lepidopterous larvae, a pair of frontal muscles (pharyngeal dilators) originates outside the cleavage lines. Snodgrass has illustrated this pair of frontal muscles in a previous paper (1928, fig. 55) and is clearly aware of their position of origin, yet he does not refer to them in his later paper (1947) when defining the frons of larval Lepidoptera, and has certainly overlooked them in formulating the rule already mentioned. The triangular area between the arms of the dorsal Λ -shaped internal ridge on the caterpillar head is called the clypeus by Snodgrass, because the cibarial muscles originate on its lower part and because he believes that the arms of the ridge, from which arise the anterior tentorial arms, represent the epistomal ridge which separates the clypeus from the frons in more primitive insects. He accounts for the presence of a pair of frontal muscles that originate on the upper part of the facial triangle by suggesting that they have migrated across the arms of the ridge. Hinton, on the other hand, regards the Λ -shaped ridge as a secondarily evolved strengthening invagination, developed in association with the very large occipital foramen and the resulting structural weakness of the dorsal areas of the cranium. There is no reason to suppose that the larval head of the common ancestor of the Trichoptera and Lepidoptera possessed such a ridge since it is absent in trichopterous larvae, and it therefore cannot be regarded as homologous with the epistomal ridge of more primitive insects. Hinton also claims that the presence of the pair of frontal muscles on the apical part of the facial triangle shows that it cannot be termed the clypeus. He considers the facial apotome, bounded laterally by the dorsal cleavage lines, to be a fronto-clypeal area on which the internal strengthening ridges, or their external grooves, do not separate the frons from the clypeus. This interpretation appears to be preferable to that of Snodgrass. Hinton's views have been criticised by Short (1951) chiefly on the grounds that they cast doubt on the value of Snodgrass' criteria for recognising the frons and clypeus in the various orders of insects. This criticism appears to be unjustified, since Hinton's views are based on acceptance of these criteria, and he differs from Snodgrass only in the conclusions he draws from an application of the criteria to the particular problem of the homologies of the dorsal cranial areas of caterpillars. Short also states that Snodgrass' terminology is applicable throughout all insect orders and claims that it is therefore preferable to that of Hinton, which only applies to the Lepidoptera. But, as Hinton has pointed out, Snodgrass has misapplied his terms to the facial areas of caterpillars, and therefore Short's claim is invalid.

3. SUMMARY.

The last instar larva of *Tipula livida* van der Wulp, a recent addition to the British list, is described. The extent of the fronto-clypeal region of the larvae of Tipulinae is discussed. In two species of *Tipula* exceptions are found to Snodgrass' (1947) general rule that the dorsal cleavage lines on the insect head always separate the origins of the facial muscles from those of the mandibular and maxillary muscles. The views of Snodgrass (1947), Hinton (1948) and Short (1951) on the fronto-clypeal region of lepidopterous larvae are discussed.

4. ACKNOWLEDGMENTS.

I wish to thank Dr. H. E. Hinton for his help in discussion and in the preparation of this paper. This work was done during tenure of a grant from the Agricultural Research Council.

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SOME OBSERVATIONS ON GROWTH AND EGG PRODUCTION OF THE BLOOD-SUCKING REDUVIID, *RHODNIUS PROLIXUS* AND *TRIATOMA INFESTANS*.

By A. J. P. GOODCHILD, B.Sc., D.I.C., F.R.E.S.

(London School of Hygiene and Tropical Medicine, Keppel St., London, W.C.1.

INTRODUCTION.

THE experiments described in the present communication were undertaken as part of a scheme of research into the relation of the blood-sucking habit in the Reduviidae to the predatory habit in other members of the family. In connection with this study, experiments were carried out to investigate the comparative efficiency as blood-sucking insects of the two species *Rhodnius prolixus* and *Triatoma infestans* by comparing the increase of weight during nymphal growth and the egg production of the adult with the weight of the corresponding blood meals. This work is largely a development and extension of an earlier study by Buxton (1930), and in the part dealing with nymphal growth the results from the present work on *Triatoma infestans* are compared with figures published by Buxton (from experiments by V. B. Wigglesworth) for *Rhodnius prolixus*. The information on egg production in relation to weight of blood meal is, for both species, the result of the present investigation.

METHODS.

The insects which were being studied were kept in 2 in. $\times$ 1 $\frac{1}{4}$ in. specimen tubes closed by a layer of mosquito netting. Adult bugs for egg production experiments were segregated into pairs, except for a few trials with *R. prolixus* in which the effect of crowding and of different sex ratios was investigated. Nymphs were studied in groups of about a dozen. Whole groups were weighed immediately before feeding, and from this weight the average unfed weight was calculated. The tubes were then applied to the ear of a rabbit, and when most of the insects had fed, all fully engorged specimens were removed and weighed to give the average fed weight. The number of nymphs in these samples was usually between six and nine. Each tube was returned to the source of food until the remaining nymphs had engorged, so that as many as possible would moult to the next instar simultaneously. The variation in fed weight of individuals was found to be small enough for the sample mean to be taken as the group mean. In the later instars, when the nymphs were larger, it was sometimes more convenient to obtain the unfed weight by a similar sampling method. The insects were offered food on the fourth or fifth day after ecdysis, and the increase in body weight was obtained from the difference between the unfed weights in consecutive instars. The adults were also weighed before and after feeding, and the eggs laid were recorded daily. The insects were incubated at 25–26° C.

RESULTS.

Nymphal Growth.

This part of the work dealt only with *T. infestans*, as stated above, and the results are set out in Table I in a similar manner to the figures presented in Buxton (1930), for convenience of comparison. The column headed "Ratio" deals with the relation of weight of blood taken to the unfed weight of the insect. For the first instar of *T. infestans*, this figure is very much less than that for *R. prolixus*, which takes about twelve times its own weight of blood in that instar. For the other instars, the difference is less striking, and some batches of *T. infestans* exceed the figures for *R. prolixus*. The continuation of the *T. infestans* figures beyond the third instar is hampered by the infrequency with which they could be induced to gorge themselves completely at one meal. Many individuals in their fourth and fifth instars also failed to moult even though apparently fully fed. With these, a further meal was given after the normal time for moulting had expired, and in most cases they moulted normally at the appropriate time after the second meal. The normal time lapse from feeding to moulting was : first instar, 9–11 days, second instar, 14–16 days, third instar, 14–16 days. For the fourth instar, the following records were obtained : one batch of six nymphs went 27 days after their first meal, were fed again, and moulted after a further 11–12 days ; another batch fed twice with a two-day interval moulted 16–18 days from the second meal ; a group of eight fourth instar nymphs moulted 14 days after their first meal, but in their case it must be noted that they had failed to moult as third instar nymphs, and had received an additional meal in that instar. They were found to be well above average weight for fourth instar nymphs, and also took more than the usual amount of blood. The exact figures are : unfed, 36.43 mg., fed, 222.75 mg., while two other groups of six fourth instar nymphs (fed only once as third instar) were : unfed, 28.66 and 30.00 mg., fed, 170.0 and 137.5 mg. respectively. In the fifth instar, there are 42 detailed records of successful moults to the adult stage. Of these, only one (out of a group of seven apparently fully fed) moulted without an extra meal, at 23 days from feeding. Eleven insects altogether were recorded as fully engorged after one meal. They were fed again when about a month had elapsed without moulting taking place. Most of them moulted after a further 21–24 days.

TABLE I.—*Weight of blood meal of Triatoma infestans in first three nymphal instars.*

Batch No.	Instar.	Weight unfed (mg.).	Weight of blood taken (mg.).	Ratio.
1	I	1.61	8.44	5.24
	II	4.16	24.09	5.79
	III	11.25	53.03	4.71
2	I	1.40	7.60	5.43
	II	4.00	21.50	5.37
	III	9.33	51.92	5.56
3	I	1.45	7.65	5.27
	II	4.00	22.67	5.56
	III	9.47	65.86	6.95

Those not fully fed were fed again after 7–10 days, and the moult then followed the second meal by the same period of 21–24 days.

It is relevant to the purpose of the present work to determine, if possible, whether this need for extra feeding in *T. infestans* is due to lower efficiency in digesting and utilising blood as a food, or whether it is a physical inability to take sufficient blood in one meal. Failure to moult in spite of repeated feeding has been observed by Brecher and Wigglesworth (1944) in *R. prolixus* nymphs deprived, by sterile culture, of their normal symbiotic micro-organisms, and these authors regarded the extinction of laboratory cultures of certain *Triatoma* species as having a similar cause. The culture of *T. infestans* used in the present work was known to be infected with micro-organisms, and failure to moult could not be correlated with their absence from any particular individual. On the other hand, there is some evidence for the second hypothesis, that of physical inability to take large enough meals. If the weight of blood meal required to give unit increase in body weight be calculated, it is found that for the first three instars of *R. prolixus* it is 3.5 mg. of blood per mg. of growth, or a ratio of 3.5 to 1. The figure for *T. infestans* is very close to this, about 3.4 to 1. It has been possible to obtain a figure for the fifth instar of *R. prolixus*, though not for *T. infestans*. The ratio in this case is found to be 5.4 to 1. It is understandable that a greater amount of blood is needed for the more complex changes which take place at the final metamorphosis to the adult. Since the early instars of both species have similar rates of food utilisation it may be assumed that they do not differ greatly in the later stages. If this be so, the inadequacy of the first meal taken by fifth instar *T. infestans* can be clearly demonstrated. The mean weight of a large number of unfed fifth instar nymphs was found to be 89.31 mg. (This was obtained from the 42 insects mentioned above, with the addition of several which were not subsequently used in experiments). That of unfed adults of both sexes was 180.83 mg., an increase of 91.52 mg. The mean weight of the first blood meal of well-fed insects was only 195.35 mg., which, on the assumption of a 5.4 to 1 ratio, would only suffice for growth to the extent of 36.17 mg. The insects were also weighed before and after the second meal. This was always larger, with a mean of 382.12 mg., but it is noticeable that even this can only suffice for 70.76 mg. of body growth, so that both meals together contribute to the growth necessary to reach the adult weight. Wigglesworth (1934) showed that moulting in *R. prolixus* is initiated by a nervous impulse from the distended abdominal wall, which stimulates the corpus allatum. How such a mechanism could be related to the multiple feeding of the later instars of *T. infestans* is a problem which has been not dealt with in the present work. It seems possible that the moulting mechanism of this species must resemble that of phytophagous Hemiptera, which also take a succession of meals in each instar, rather than that which is believed to operate in *R. prolixus*.

In general, it may be said that a fifth instar *R. prolixus* nymph can take in one feed more than enough blood to enable it to moult to the adult stage, while *T. infestans* has difficulty in getting sufficient food in less than two feeds. If a recently moulted *R. prolixus* adult is dissected, the stomach is found to contain a good store of undigested blood, which may in some cases enable the female to lay one or two eggs without further feeding. In fact, if nymphs of this species are fed more than once in the fifth instar such egg laying is almost certain to

take place. This has been observed regularly when the insects were confined in slightly crowded conditions. The eggs have hatched normally. *Triatoma infestans*, on the other hand, so far from laying eggs without feeding in the adult stage, very often fails to lay until it has received two or even three feeds. The figures for weight of meal and egg production of *T. infestans* were compiled from records of thirty-five productive meals. There were, in addition, ten instances where no eggs were laid after the first feed, and three instances where no eggs were laid after the first two feeds. Furthermore, dissection of a newly moulted *T. infestans* adult reveals a stomach which is usually completely empty. It must be emphasised that the insects in these experiments were all fertilised, since it was observed by Buxton (1930) that oviposition was delayed until after two or more feeds when *R. prolixus* females were fed but not mated.

Egg Production.

The results of this study are summarised in Table II. It will be seen that in the case of *R. prolixus*, a mild degree of overcrowding had no significant effect on the rate of egg production, although it was under such conditions that egg laying by unfed adults was most often observed. The number of eggs

TABLE II.—Weight of blood taken and egg production.

	Max.	Min.	Mean.
<i>Rhodnius prolixus</i> .			
1. Single pairs of bugs :			
Weight of unfed female (mgm.) . . .	86	47	62·1
„ of fed female	280	161	243·7
„ of blood taken	213	114	181·5
Number of eggs laid	44	14	29·6
2. Groups of bugs :			
Weight of unfed female	86*	53*	62·6
„ of fed female	266*	212*	243·6
„ of blood taken	210*	156*	181·0
Number of eggs laid	40*	25*	30·1
Mean weight of blood taken, as percentage of mean unfed weight . . .			291·9
<i>Triatoma infestans</i> .			
	Max.	Min.	Mean.
Weight of unfed female	254	124	172·1
„ of fed female	529	315	410·2
„ of blood taken	307	139	238·1
Number of eggs laid	19	1	8·1
Mean weight of blood taken, as percentage of mean unfed weight . . .			138·3

* Mean of females in group.

produced by *T. infestans* for each blood meal taken is much less than that obtained from *R. prolixus*. One reason for this is the smaller meal, in relation to its body size, which is taken by *T. infestans*, as is shown in the tabulated data by the mean weight of the meal expressed as a percentage of the mean unfed weight. It is possible for *R. prolixus* to take a larger meal in proportion to its

size because the pleural region of the abdomen is partly unsclerotised and can stretch considerably, whereas that of *T. infestans* is not able to do so (fig. 1). It may be remarked that in the adult bed-bug (*Cimex lectularius*), representing another family of blood-sucking Hemiptera, the abdomen, when fully fed, extends longitudinally as a result of the stretching of the inter-segmental membranes. In this case the same result as in *R. prolixus* is achieved in a slightly different way.

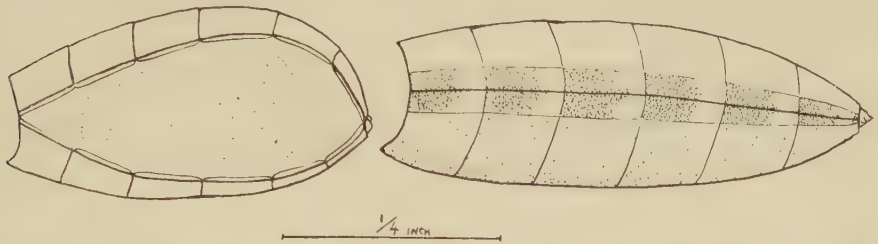


FIG. 1.—The fully engorged abdomen of the adult of *Rhodnius prolixus* (on left) and *Triatoma infestans* (on right) showing the extension of the pleural region of *R. prolixus*.

In order to determine whether there is any difference between *R. prolixus* and *T. infestans* in the efficiency with which the ingested blood is metabolised, the available information must be examined more closely. First of all, the figures for egg number are converted into weight of eggs produced. The weight of a single egg of *R. prolixus* is 0.75 mg. and that of *T. infestans* is 2.0 mg. In fig. 2 the relation of egg weight to weight of blood taken is shown graphically for both species. The data used in calculating the regression line for *T. infestans* included those meals which did not result in oviposition in addition to the figures given in Table II. These regression lines can be extrapolated to the point of zero egg production. The value of blood meal weight for zero egg weight is 149.5 mg. for *T. infestans*, compared with 50.9 mg. for *R. prolixus*. This may be regarded as the amount of food needed for body maintenance only during each cycle of feeding and oviposition. It may be expected to be greater in the larger insect, and when the same figure is expressed as a percentage of the unfed adult weight, it becomes 81.4 per cent. for *R. prolixus*, and 88.2 per cent. for *T. infestans*. The difference between the two species would be even less if the food retained by *R. prolixus* from the previous instar could be estimated.

It would seem permissible, therefore, to assume that the maintenance requirements of the two species are similar, and by subtracting that amount from the total, to isolate that portion of the ingested food which is directly concerned with egg production. When this is done, the regression lines of the two species (fig. 2) are reduced to the same origin, and it is found that they will almost coincide, since their slopes do not differ significantly. This indicates that the two species are almost equally efficient in the utilisation of their food.

One further point remains to be considered, and that is the possibility that greater numbers of eggs are produced as a result of a reduction in the weight of the egg relative to the weight of the adult insect. It can be shown that this is not the case with the two species here studied, since the egg weights are in the ratio 2.700 to 1, and the unfed adult female weights in the ratio 2.715 to 1, and

even this very slight difference is in favour of *T. infestans*, rather than the more productive *R. prolixus*.

It can be said, as a result of this analysis, that the greater egg production of *R. prolixus* is due entirely to the structural adaptation which enables it to take larger meals, and not to any increase in metabolic efficiency.

Since *T. infestans* is handicapped in such a way, it seemed possible that a compensating effect might be found in the feeding behaviour, so that this species might feed more frequently if food were constantly available. In all the past work, as in the experiments so far recorded here, the insects were given

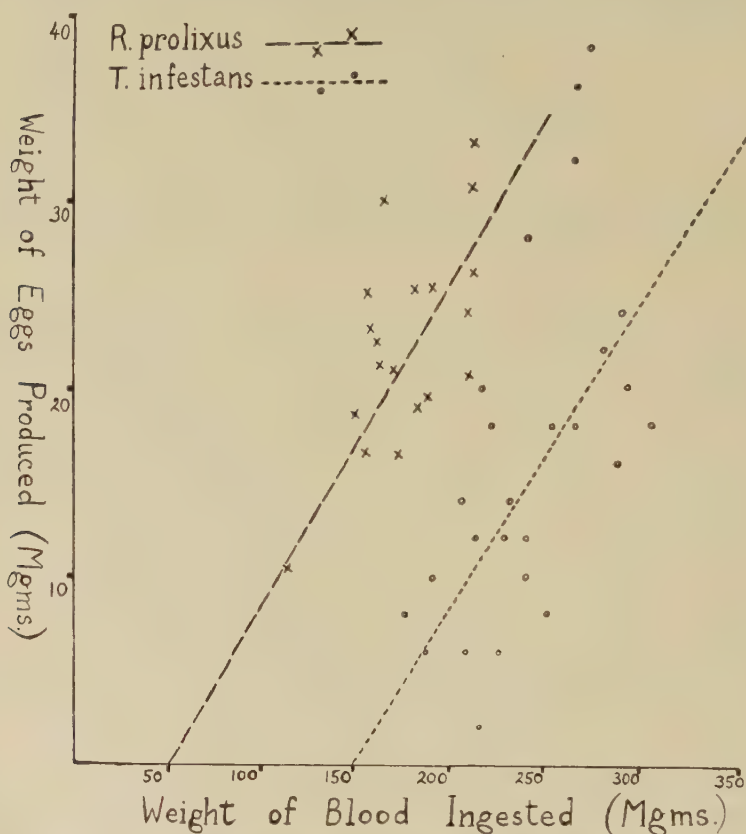


FIG. 2.—Graph illustrating the relation between egg production and weight of blood taken in *Rhodnius prolixus* and *Triatoma infestans*.

one full feed, and then were not fed again until oviposition had ceased (or, in some specimens of *T. infestans*, until a time sufficient for oviposition had elapsed, even though no eggs were laid). Another experiment was set up in which the insects were offered food as near daily as was possible. When this was done, it was found that both species fed on one-third to one-half of the opportunities presented, and that the rate of egg production was correspondingly increased, in *R. prolixus* no less than in *T. infestans*. Five pairs of *R. prolixus* and eight

pairs of *T. infestans* were used, and in the fifty days' duration of the experiment, the average number of feeds per insect was 17, out of 37 opportunities offered for *R. prolixus*, and 12 times out of 28 for *T. infestans*. These figures refer to the females only, no record being made of the feeding of males. The average egg number in fifty days was 128.8 from *R. prolixus* and 47.6 from *T. infestans*. It is interesting to note that in terms of egg weight the rate of production is very similar (about 96.6 mg. and 96.3 mg. respectively). With *R. prolixus* it was especially noticeable that feeding occurred even when the female bore a load of ripe eggs, and that in these circumstances, oviposition followed close upon feeding, no doubt as a result of the increased internal pressure. The number of eggs laid by the insects after the last feed, when the experiment was being terminated, was found to be very much larger than the egg number from a single meal, being an average of 49.2 for *R. prolixus* and 22.9 for *T. infestans*. This seems to indicate that the egg production recorded in this experiment is the maximum possible at that temperature (25–26° C.), and that food was being taken at a rate exceeding its utilisation. It was not practicable to measure the weight of blood ingested during this experiment, and the comparison of the two species was on the basis of frequency of feeding and egg production in unit time. As has been stated, there was no significant difference between them, and the compensating effect expected in *T. infestans* was not found to occur.

SUMMARY AND CONCLUSIONS.

The two species of blood-sucking Reduviidae, *Rhodnius prolixus* and *Triatoma infestans*, have been studied from the viewpoint of their degree of adaptation to the blood sucking mode of nutrition. The relation of nymphal growth and adult egg production to the weight of blood ingested was used as the basis of comparison, with the following results :

1. The increments of nymphal growth per unit of blood meal taken are the same in *T. infestans* as in *R. prolixus* (latter figures from Buxton, 1930), but in the later instars of *T. infestans*, a smaller food capacity makes it necessary for the insect to take more than one meal before it can moult. The fifth instar nymph of *R. prolixus* not only takes enough food in one meal for it to moult to the adult, but may retain sufficient unused food to enable the adult female to lay one or two eggs without further feeding. The occurrence of oviposition under these circumstances has not previously been recorded. The eggs laid were found to be fertile.

2. Although the adult female of *T. infestans* lays a much smaller number of eggs per blood meal than *R. prolixus*, an analysis shows that this is entirely due to the greater capacity for food of the latter species. A structural adaptation is present in the abdomen of *R. prolixus*, which enables it to take larger meals in relation to its body weight.

3. In spite of the smaller food capacity of *T. infestans* adults, they do not feed more frequently than *R. prolixus* when the source of food is continually present. Under such conditions both species will feed about every third day. It would appear, therefore, that the rate of increase of *T. infestans* in a natural infestation must always be lower than that of *R. prolixus*. This study shows that *T. infestans* is less well adapted to the blood-sucking habit than *R. prolixus*.

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This work was done under the direction of Professor P. A. Buxton, to whom I am indebted for advice and encouragement, as I am also to other members of the staff of the Entomology Department of the London School of Hygiene and Tropical Medicine, and to members of the staff of the Statistics Department for help with that aspect of the work.

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FACTORS INFLUENCING SMALL-SCALE MOVEMENTS OF SOME BRITISH GRASSHOPPERS.

By J. P. DEMPSTER, Ph.D., D.I.C., F.R.E.S.

INTRODUCTION.

DURING the summers of 1952 and 1953, an investigation into the factors influencing movement in grasshoppers was undertaken at the Imperial College Field Station, Sunninghill. This was a direct continuation of work described by Richards and Waloff (1954), though the design of the experiments was somewhat different.

A. Small-scale movements of nymphs of Chorthippus parallelus (Zett.).

Alternate plots similar to those designed by Richards and Waloff (1954) (fig. 1) were erected on an almost pure stand of *Holcus mollis*. Three alternative

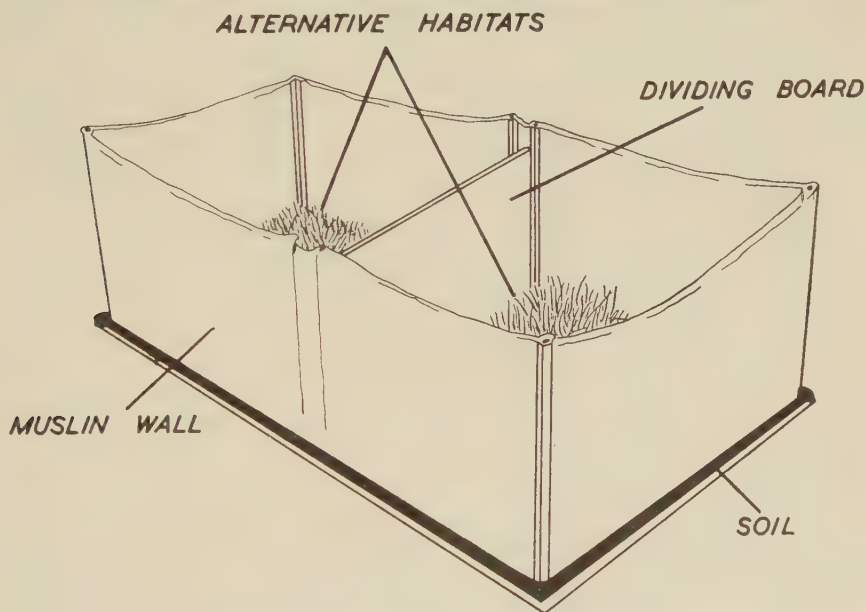


FIG. 1.—One of the nine enclosed pairs of plots.

habitats were considered : (1) grass about 6–9 inches high, (2) grass cut to within an inch of the ground, and (3) bare ground with an occasional tuft of long grass left to prevent lack of food influencing movement.

By erecting the plots on a slope of about one-in-six, the effect of slope on movement could also be seen. Thus nine enclosures were made, containing every combination of the three habitats and slope, as follows :

Top (North).

Bare	Short	Long	Bare	Short	Short	Long	Bare	Long
Bare	Short	Long	Short	Bare	Long	Short	Long	Bare

Bottom (south).

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Eight third or fourth instar hoppers were marked with artists' oil paint and released in each half, a different colour being used on hoppers released in different habitats. After being left undisturbed for 24 hours, each enclosure was carefully divided down the middle by a board, and the numbers in each half counted. From these counts the number leaving and entering each alternative was obtained, and this was used as a measure of the reaction of the hoppers to the different conditions.

Unfortunately, some hoppers moulted during the experiments and so lost their marks. However, over the whole series of experiments the effect of loss of hoppers in this way should be random. Some hoppers escaped from the enclosures and these were included with the numbers leaving the alternatives.

Between 11th June and 22nd July, 13 sets of data were obtained, and the results are shown in Table I.

TABLE I.

(a) *Numbers leaving each alternative.* (b) *Numbers entering each alternative.*

	Bare.	Short.	Long.			Bare.	Short.	Long.	
Top	201	160	122	483	Top	14	16	46	76
Bottom	199	144	121	464	Bottom	17	45	57	119
	400	304	243	947		31	61	103	195

(i) *The effect of length of grass on movement.*—An analysis of variance carried out on the above figures shows that there is a significant difference between columns (0.01–0.05 level) when considering both numbers leaving and numbers entering each alternative.

(ii) *The effect of slope on movement.*—An analysis of variance between rows of the figures above shows no significant effect of slope. The significance of the means of the basic data was therefore tested. This showed a significant effect of slope on the numbers entering short grass only. That is to say, significantly more hoppers entered the short grass at the bottom of the slope than at the top.

(iii) *The effect of drought on movement.*—When the series of experiments was started the condition of the grass was very good. By the end of July, however, continuous hot weather had caused the grass to become dry and yellow. This was particularly noticeable in the case of the short grass. For this reason a comparison of data obtained between 11th and 25th June, and 13th and 22nd July, was carried out. (cf. Table II.)

TABLE II.

(a) *Numbers leaving each alternative before 25.vi. (results from 4 experiments).* (b) *Numbers leaving each alternative after 13.vii. (results from 4 experiments).*

	Bare.	Short.	Long.			Bare.	Short.	Long.	
Top	49	33	23	105	Top	67	60	48	175
Bottom	52	31	30	113	Bottom	63	61	48	172
	101	64	53	218		130	121	96	347

In the short-grass sections, there was a significant increase in the number leaving (0.001–0.01 level) and a decrease in the number arriving (0.001 level) after the drought. The same is seen in the case of the long-grass and bare sections, but to a less marked extent.

B. *Small-scale movements of adults of C. parallelus and C. brunneus.*

In 1953 it was decided to carry out a similar set of experiments on the adults of *Chorthippus parallelus* (Zett.) and *Chorthippus brunneus* (Thunb.) (= *C. bicolor* Charp.) This time, however, only two types of habitat, long and short grass were used. Also the effect of orientation was considered by erecting four alternate plots (each combination of habitat and slope) on a north-facing and a south-facing slope. Further, the effect of time of day was also investigated by carrying out the experiment twice daily, leaving the grasshoppers in the enclosures for four hours at a time. In this way the effect of four variables (length of grass, slope, orientation and time of day) on movement of the grasshoppers was observed.

Unfortunately the number of grasshoppers available was limited, and the number entering each alternative was too small to show a significant effect of any of the factors being considered.

When comparing the numbers leaving each alternative it was found that only the length of grass had a significant effect (at 0.05 level) on movement.

The number of both species leaving long and short grass is shown in Table III.

TABLE III.—*The number of C. parallelus and C. brunneus leaving long and short grass.*

	<i>C. parallelus.</i>		<i>C. brunneus.</i>	
	♂.	♀.	♂.	♀.
Long grass .	131	135	77	93
Short grass .	158	112	107	93

It will be seen that in *C. parallelus* more males left the short than the long grass, while more females left the long than the short. *C. brunneus* males similarly showed a greater movement from the short than from the long grass, but length of grass had no significant effect on the movement of the females.

In *C. parallelus* and *C. brunneus* the significance of the interaction between orientation and slope was very near the 0.05 level of significance. The possible reason for this will be discussed later.

C. *A comparison of conditions of temperature and humidity in each of the alternative habitats.*

For this work fine thermocouples of 38 S.W.G. copper and constantan wire, with 20 S.W.G. leads, were used. These passed through a common cold junction of ice and water to a portable potentiometer. For all readings the thermocouples were shaded from direct solar radiation by aluminium shields.

(i) *Temperature*.—To measure the temperature within the sites, the thermocouples were arranged in pairs so that air temperature (9 in. above ground level)

and ground-level temperature ($\frac{1}{4}$ in. above the ground) could be recorded from one site. Air and ground-level temperatures were recorded alternately, as rapidly as possible, so that a series of air temperatures with corresponding ground-level temperatures were obtained for each habitat.

There was a great deal of variation between readings, due to wind, amount of cloud, etc., but over the range of temperatures observed, there was a significant difference between ground-level temperatures (to 0.0001 level) in the different habitats. It will be seen in Table IV that with an increase in vegetation there is a decrease in the ground-level temperature.

TABLE IV.—*Average air and ground-level temperatures in each of the habitats.*

Habitat.	Number of observations.	Average air temp. °F.	Average ground-level temp. °F.
Bare ground . .	82	84.4	102.0
Short grass . .	101	82.6	97.1
Long grass . .	69	84.6	95.3

It is interesting to compare the temperatures in short grass when green and when dried. As is seen in Table V, dried short grass tends to be far hotter than green short grass, and tends in fact not to be significantly cooler than bare ground. This comparison was made by measuring temperatures in short grass that had remained green on account of shading by the walls of the enclosure, and short grass that had become dried and yellow.

TABLE V.—*Average air and ground-level temperatures in green and dried short grass.*

Habitat.	Number of observations.	Average air temp. °F.	Average ground temp. °F.
Green short grass .	48	83.9	94.2
Dried short grass .	53	81.1	100.3

(ii) *Humidity*.—At first ventilated wet and dry-bulb thermometers (Assman Psychrometer) were used, but the area of each habitat was so small that it was suspected that air was being drawn from outside the habitat. For this reason this method was abandoned, and wet and dry shielded thermocouples were used.

About 40 readings were taken in each habitat and the maximum and minimum readings so obtained are shown in Table VI.

TABLE VI.—*Maximum and minimum relative humidity readings in each habitat.*

Habitat.	Min. relative humidity. %.	Max. relative humidity. %.
Bare ground . . .	39	73
Short dried grass . .	42	72
Short green grass . .	39	88
Long grass . . .	53	96

DISCUSSION.

It is seen from the first series of experiments that *Chorthippus parallelus* nymphs tend to move from short to long vegetation. A similar tendency was observed in the 1950 series of experiments by Richards and Waloff (1954) for *C. brunneus* nymphs. It seems possible from Tables IV and VI that this may be a movement from the hotter and drier habitat.

This tendency is again apparent when the effect of drought is considered. It was seen in Table II that there was an increase in the number leaving short grass after the drought. Tables V and VI indicate that this may also be an increased movement from the hotter, drier habitat.

The first series of experiments showed that slope had no significant effect on the movement of nymphs, except in the case of short grass. Here, significantly, more hoppers entered the short grass at the bottom of the slope than at the top. This was most probably due to the fact that the short grass remained noticeably greener at the lower end of the compartment, where it was shaded by the muslin side of the enclosure during the dry weather. This may well have affected the number of nymphs entering the lower compartment. This suggestion is supported by the fact that slope had no significant effect on movement before the drought.

The second series of experiments indicates that males of *C. parallelus* and *C. brunneus* show a similar tendency to move into longer vegetation. The females of *C. parallelus*, however, show a reverse tendency, while *C. brunneus* females showed no tendency for differential movement.

The effect of shading by the muslin at the southern end of the enclosures is seen once again in the second series of experiments. Both these species of *Chorthippus* are sun-loving insects and thus tend to move out of the shaded area of the enclosures. This area was larger on the north-facing slope than on the other (fig. 2), so that more grasshoppers moved downhill on the north-facing

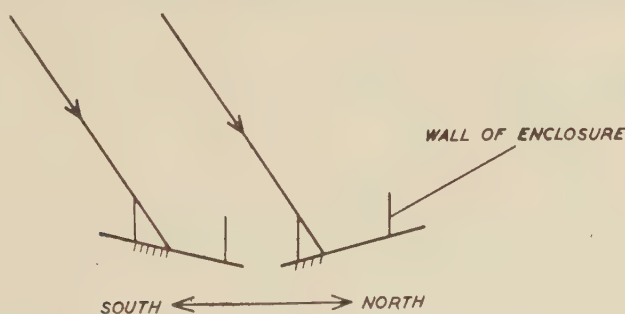


FIG. 2.—Illustrates the greater area shaded by the wall of an enclosure on the north-facing slope.

slope than uphill on the south-facing one. This movement probably caused the interaction of orientation and slope to be very near the 0.05 level of significance in a variance ratio test.

Unfortunately, the number of adults of *C. parallelus* and *C. brunneus* available for the second series of experiments was limited, and the effects of the different factors on movement are not as clear as one might have wished. The

results obtained, however, agree with observations made by Richards and Waloff (1954), who showed that there was a general movement of the nymphal populations of *C. parallelus* and *C. brunneus* from the more open vegetation of the main area of Colony 2, into the long stand of *Holcus mollis* in the strip below. Further, evidence was obtained of a substantial uphill return movement of the females.

SUMMARY.

Experiments designed to investigate the factors influencing small-scale movements of *Chorthippus parallelus* and *Chorthippus brunneus* are described. Of the factors that are considered, only the length of vegetation was shown to have a significant effect on movement. Nymphs and adult males tended to move from short into long vegetation, while females of *C. parallelus* showed a reverse tendency.

ACKNOWLEDGMENTS.

This work was carried out at Imperial College Field Station, Sunninghill, Berks, and I am deeply indebted to Prof. O. W. Richards and to Dr. N. Waloff for their help and encouragement. I also wish to thank Dr. B. P. Uvarov of the Anti-Locust Research Centre for advice, and for the award of a scholarship which enabled this work to be carried out. Finally, I wish to thank Mr. J. W. Siddorn for his advice and help in obtaining measurements of temperature and humidity in the field.

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VARIATION IN THE MALE SECONDARY SEXUAL CHARACTERS OF
THREE AFRICAN SPECIES OF *ZYRAS* STEPHENS (COLEOPTERA :
STAPHYLINIDAE).

By The Rev. C. E. TOTTENHAM, M.A., F.R.E.S.

AMONGST Staphylinid material kindly sent to me by Mr. V. F. Eastop during the last two years from Kenya, three species of *Zyras* have been in sufficiently large numbers to make it possible to study the range of variation in the male secondary sexual characters. The insects were taken partly by general collecting, a few of the *Z. schuberti* with a species of *Odontotermes*, but the majority by means of light traps.

In these three species, and in a fourth plentiful species not possessing sexual characters of the same type, the females appear to be more abundant than the males, as may be seen from the following figures :

<i>Sex Ratios.</i>			
	Total number of specimens.	Males.	Females.
<i>Z. hamifer</i> Fauvel	265	93 (35%)	172 (65%)
<i>Z. usambarae</i> Bernhauer . .	359	149 (41·5%)	210 (58·5%)
<i>Z. schuberti</i> Bernhauer . . .	1553	620 (40%)	933 (60%)
<i>Z. maculipennis</i> Bernhauer . .	1725	827 (48%)	898 (52%)

The three species studied all possess male secondary sexual characters on the upper side of the third (first wholly visible) abdominal segment. In two of these species, *hamifer* and *schuberti*, the extreme forms of these characters are so different that, were it not for the intermediate forms, it would appear that there were two distinct species in each case.

In the following descriptions numbers refer to the true abdominal segment, thus tergite 3 is the tergite of the third (first wholly visible) segment.

Zyras maculipennis Bernhauer.

The male secondary sexual characters of this insect do not lend themselves to measurement and consequently any statistical analysis would be very difficult. The apical margin of tergite 3 is somewhat triangularly raised in the middle. The maximum height is about one-third the width of the tergite ; at the other extreme the elevation can scarcely be detected. Variation occurs in the slope of the raised margin and in the extent to which the elevation extends along the length of the tergite. The whole range of form could be summarised as being the same as that which would be seen if a rectangular piece of material were placed on a slightly arched surface and (a) the middle of one edge were raised to various heights and (b) this were done with material of different weights. In addition to such variation are two unusual forms. In the one the slope of the elevation suddenly becomes abrupt near the apex and the apex is in the form of a slightly flattened arch. Whereas in normal forms the margin, if

viewed from above, would appear more or less straight, in the other unusual form the margin is clearly produced from each side and then very broadly and distinctly emarginate in the middle, the emargination showing a slightly bisinuate character.

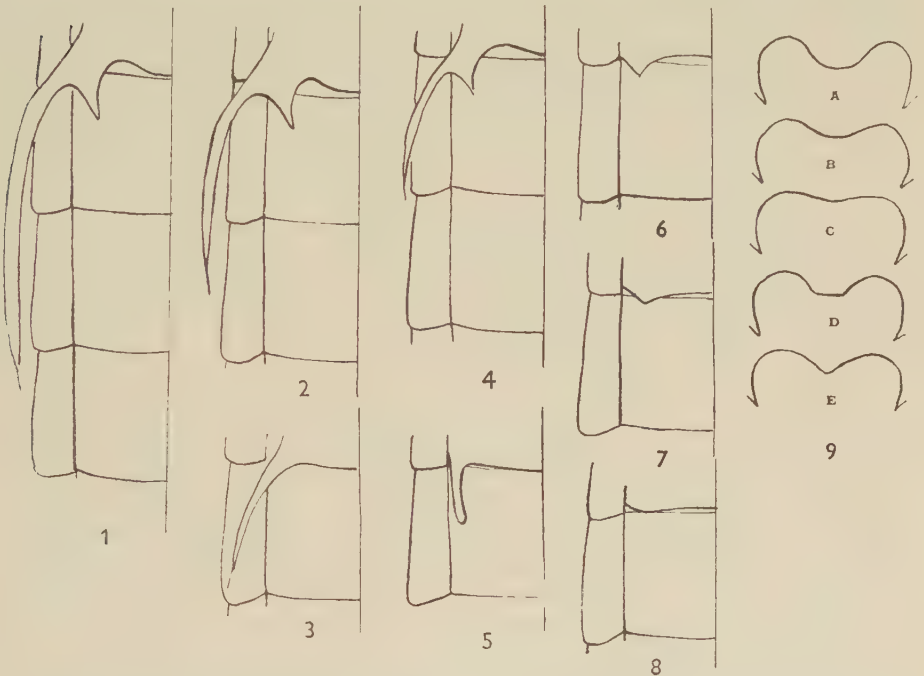
Zyras schuberti Bernhauer.

In this species the commonest form of the males exhibits a long prong extending down each side of the abdomen for about the length of two segments. These prongs arise from the posterior corners of tergite 3; at their bases, on the inner side, they are strongly curved into an inwardly pointing tooth; the margin of the tergite between the prongs is bisinuate. Variation is found in (a) the length of the prongs, (b) the form of the tooth and its presence or absence, (c) the sinuosity of the margin. The common form is shown in fig. 1. The fact that the prongs begin basally in curves renders exact measurement difficult; comparison with the length of the abdominal segments is not wholly accurate since the segments may or may not be telescoped; the complete range of variation makes it difficult to select suitable dividing points for grouping. The summary given in the following table gives a reasonably accurate picture of the variability of the characters.

	Prong.	Number of specimens.	Tooth.	Terminal hairs.	Margin.
50% long (figs. 1, 2)	Nearly 2 segments or more	279	Present	Present	Bisinuate, very variable (fig. 9, A-E).
	Approx. $1\frac{1}{4}$ – $1\frac{3}{4}$ segment	30	Present	Present	Bisinuate, very variable.
9% short (figs. 3–5)	About 1 segment	42	Present (30), absent (12)	Rarely absent	Bisinuate, less variable, strong, sinuities absent (fig. 9, B, C).
	Half segment or less	27	Absent	Absent	Straight or feebly concave (bisinuate in 2).
41% absent (figs. 6–8)	Trace	70	.	.	Straight or feebly concave (bisinuate in 1).
	No trace, only angle	172	.	.	Straight or almost straight.

All the long-pronged forms (figs. 1, 2) possess the basal tooth. The degree of sinuosity of the margin is variable; rarely it is very slight, (less than fig. 9, c) and occasionally the central arch is triangular (fig. 9, e) or truncate (fig. 9, d). All the long forms also possess apical hairs. The tooth varies but little; it is usually sharp, sometimes rather blunt, but always well-formed. In the short-pronged forms the basal tooth is present in more than half the specimens with the prong about one segment in length (fig. 4), but absent when the prong is less than a half segment (fig. 5). In these latter the terminal hairs have also disappeared, whereas they are present in the majority of the former group of short prongs. Amongst the short prongs the margin is bisinuate in the one-segment length group (fig. 9, B, c), but not showing the very sinuate forms of the long-pronged group, while in the half-segment lengths it has become nearly always

flat or a little concave (figs. 5, 6). In the group with no prongs, it is very difficult to draw a distinction between those with (fig. 6) or without (figs. 7, 8) traces of prongs. In all except one specimen the margin has lost its sinuous character and become straight or feebly concave. The exceptional specimen, however, has the trace of prong very blunt and should possibly be classed as a short-pronged form, the prong being as short as its width. It would be interesting to study the forms in which the prong-length varies from one-half to one segment, for it is amongst these that the apical hairs disappear, the basal tooth disappears and the margin loses its sinuosity; but to obtain a series of 100 specimens



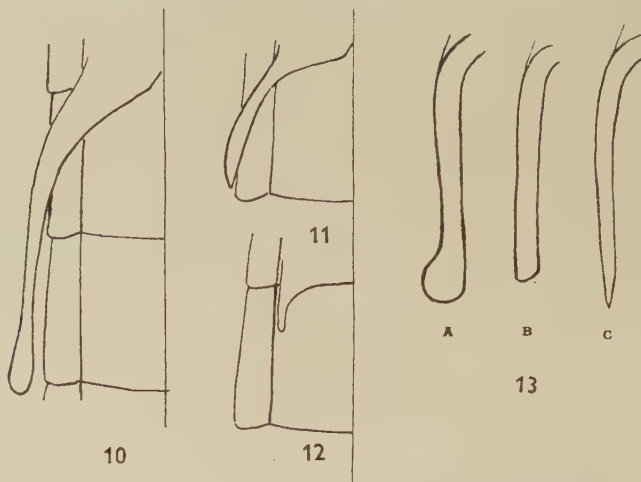
FIGS. 1-9.—*Zyras schuberti* Bernhauer. (1, 2) Long prongs; (3-5) short prongs; (6-8) no prongs; (9) variation in margin of tergal plate.

within the required range would involve the capture of about 8000 specimens. A comparison of the very short-pronged forms (fig. 5) with the very long (fig. 1) might suggest that the short prong was in reality the basal tooth; but the fact that the tooth completely disappears in some of the one-segment length forms points to its being a prong, and its being parallel or convergent instead of divergent may be due to the absence of tooth.

Zyras hamifer Fauvel.

This species also possesses abdominal prongs but without basal teeth. The inner basal edges of the prongs are curved and meet or almost meet in the centre of the margin, forming a broad curve or very obtuse angle (figs. 10, 11); at the centre the margin is generally distinctly triangularly excised, but occasionally

the excision is absent. In the forms where the prongs are very short (i.e. less than one-half segment in length) the margin often becomes straight and the excision is slight or absent (fig. 12). The prongs themselves vary in length as in the previous species, but are never absent, occasionally they exceed two segments. They differ from those of *schuberti* in not having terminal hairs; also in some of the long forms the apex is enlarged (fig. 13, A). This enlargement is a little variable, somewhat circular or oval; it appears as a disc in the vertical plane



FIGS. 10-13.—*Zyras hamifer* Fauvel. (10-12) Variation in length of prongs; (13) lateral aspect of prongs, A laminate, B truncate, C pointed.

(more or less); the expansion of the prong into this disc takes place on the upper edge only. These laminate forms have been regarded as a different species from those in which the prongs are pointed (fig. 13 C); but I can detect no other differences between the insects and I have two intermediate specimens in which the prong is not pointed but broadly truncate at apex (fig. 13 B). The 78 males examined could be grouped:

Prongs laminate, long	.	.	.	.	.	25
„ truncate, long	.	.	.	.	.	2
„ pointed, long	.	.	.	.	.	27
„ pointed, short (one segment or less)	.	.	.	.	.	22
„ pointed, short (half segment or less)	.	.	.	.	.	17

LARVAE OF SOME EAST AFRICAN TRICHOPTERA.

By N. E. HICKIN, Ph.D., F.R.E.S.

INTRODUCTION.

IN many parts of the world larvae, pupae and adults of Trichoptera form a not inconsiderable part of the food of various species of freshwater fish. In addition, Trichoptera often occur in such large numbers that their larvae play a major part in the breakdown of organic material, living and dead, in fresh water—from the cutting up of large leaves fallen into the water on the one hand to the ingestion of diatoms on the other. The larvae of Trichoptera show a wide range of form and habit and in temperate regions occupy all types of freshwater habitat. A knowledge of this group is, therefore, indispensable in Freshwater Fisheries Research.

In tropical Africa, however, the problem of preventing deterioration of existing fisheries—indeed to improve the yield of this important source of protein food—has become of great urgency. Unfortunately, work on the biology of fresh water is hampered by the almost total lack of information concerning the immature stages of aquatic insects. There are many attendant difficulties in the way of remedying this. Not only are there very few institutions in tropical Africa where work of this nature can be undertaken, but trained personnel often cannot be spared from what seems to be more urgent work in the scale of priority. In addition, the great distances and the trying tropical conditions make the collection, transporting alive, and subsequent rearing of aquatic insects an operation of great difficulty. Nevertheless, it was thought that modern air travel made it possible for living larvae of Trichoptera to be transported to England, there to be reared and subsequently described and figured (where, also, this latter work could best be done). That this was accomplished successfully is due to the Director of the East African Fisheries Research Organization, who provided a return air passage. Mr. Beauchamp also most generously made available all the facilities of the laboratory and aquarium of the East African Fisheries Research Organization at Jinja, Uganda. I am indebted also to Dr. Philip Corbet, who extended his hospitality and accompanied me to many of the collecting stations; indeed I must thank all members of the staff of E.A.F.R.O. for their help. Mr. R. C. B. Hartland-Rowe took me to the Namugongo locality mentioned below and made available to me the facilities of the Zoological Laboratory at Makerere College, Kampala. Finally I must thank Mr. J. P. C. Greenway, of the Lake Victoria Fisheries Service, for a passage up the Kagera River on the "Darter".

METHODS.

The pond net was most usually employed from bank or boat, but sometimes stones and leaves were turned over where it was possible to wade and on a few occasions a dredge was towed behind a motor launch. Two methods of transporting living caddis larvae were tried out and both were successful. In the

first place the method adopted was that usual in Europe—packing the living larvae in wet, crisp waterweed or dead leaves and then draining surplus water away. Secondly, all material was collected, waterweed and vegetable debris, that was likely to contain larvae and placed in a milk churn of several gallons capacity and about three-quarters filled with water. The churn was then transported back to the laboratory with as little delay as possible, and sorting out of the collection was then carried out. This method was used when collecting with Mr. R. C. B. Hartland-Rowe. Six species were reared in the aquarium attached to the Jinja Laboratories. About a gallon of water was placed in a large circular glass dish and a frond of *Ceratophyllum* introduced tied to a stone. One or two small plants of *Pistia* were floated on the surface to give a foothold for emerging pupae. Air was then bubbled into the water through a glass tube and, in the case of Hydropsychidae, the amount of air was sufficient not only to aerate but to cause considerable water movement. The glass dishes, after introduction of the larvae, were covered with mosquito netting held down with rubber bands and labelled.

Larvae of four species were transported to England alive by air by the method first described—three species of *Leptocerina* and *Anisocentropus usambarensis* Ulmer. Adults of two species of *Leptocerina* emerged from my aquaria at Bletchingley. Larvae of *Leptocerina ugandana* (Ulmer) and *Anisocentropus usambarensis* Ulmer lived for some weeks in an unheated aquarium but did not mature.

Failure overtook attempts to keep larvae alive on board the “Darter”. Three species were placed in large shallow trays (see *Kagera Bay*) but with the violent pitching of the boat in various circumstances water and larvae were lost overboard! The milk churn method, with aeration by compressed air, would probably be successful.

COLLECTION OF ADULT TRICHOPTERA.

A collection of adult Caddis Flies was made. Not very much time was available for beating overhanging vegetation in the larval localities, but, nevertheless, a few specimens were obtained in this manner. By far the greater number were, however, obtained at light. The lights of the “Darter” were productive and very convenient. The collection has been presented to the British Museum (Natural History) and is being worked on by Mr. D. E. Kimmins, who identified the adults of all the larvae described in this paper.

LOCALITIES VISITED.

A search was made for the larvae of Trichoptera in the localities listed below, all in Uganda with the exception of Kyaka in Tanganyika. The province is given and the approximate height above sea level in feet.

Bugungu drainage ditch. Near Jinja, west side of Napoleon Gulf. (Mengo. 3,500.)

24.v.54. Roadside drainage ditch, temporary water; many aquatic insects and fish. No Trichoptera collected.

Bujiagali. On east bank of Victoria Nile below Owen Falls. (Busoga. 3,500.)

Buyende. Small, temporary, circular, shallow pool on clay. (Busoga. 3,000.)
26.v.54. An isolated pool in a dry region; water temperatures sometimes in the region of 40° C. Larvae of Odonata but no Trichoptera collected.

Entebbe. Botanic Gardens. (Mengo. 3,500.)

5.vi.54. A sheltered, secondarily-wooded park area near the lake-side.

Jinja. Lake-shore near pier. (Busoga. 3,500.)

Open, grass-covered, shallow margin to lake. Region regularly cleared of rooted aquatic plants for malaria control, but, although a search was made on many occasions during May 1954 amongst the cleared plants, no larvae of Trichoptera were collected. Adults of a number of species were collected at light from the Laboratory windows nearby.

Kagera Bay. (Masaka. 3,500.)

11-19.v.54. A lagoon-like area where the River Kagera runs into the western shore of Lake Victoria at the Southernmost tip of Uganda. It is protected from wave action by Busungwe Island. A number of collections were made amongst the aquatic vegetation but no larval Trichoptera were found, although a number of adults came to light. About two miles south of the East African Marine Company's Pier on the mainland opposite the southern end of Busungwe Island, two small streams ran into the lake, and from these streams larvae of three species were collected. It was not possible to rear them, however, but two were Leptoceridae (one with a spirally-formed case reminiscent of the European species *Triaenodes bicolor* Curtis, and one with a case of square cross-section reminiscent of the European species *Lepidostoma hirtum* F.). The other larva was probably a Polycentropid.

Kyaka. (Tanganyika. 4,000.)

17.v.54. The River Kagera may here be crossed by pontoon ferry. A collection of aquatic insects made from the North bank which is very steep, contained only one larval Trichopteron (unidentified).

Namugongo River. (Mengo. 4,000.)

9.v.54 and 4.vi.54. Small stream flowing through sparsely-wooded marsh. This was a most productive locality. Larvae of *Leptocerina ugandana* (Ulmer), *L. ramosus pinheyi* Kimmins and a new subspecies of *L. ramosus* were collected there.

Nawanga River, near Busembatia. (Busoga. 4,000.)

28.v.54. Sluggish, exposed river winding through a wide Papyrus swamp. A very productive habitat for aquatic beetles. Fairly dry country with much cultivation of oranges. No Trichoptera collected.

Nyenga forest stream. (Mengo. 4,000.)

2.v.54 and 22.v.54. Fast-flowing, permanent, shallow, narrow stream passing through part of the southerly region of the primary, montane Mabira Forest. Trichoptera collected: Adults of *Anisocentropus usam-*

barensis Ulmer were taken on the wing and resting in a culvert where the stream flowed under the path. The larvae were searched for but not found, but two unidentified larvae were found.

Ripon Falls. Jinja. (Mengo. 3,500.)

27.v.54. The source of the Victoria Nile at the Northernmost end of Napoleon Gulf in Lake Victoria. Trichoptera collected: Adults and larvae of *Phanostoma senegalense* Brauer and *Cheumatopsyche* new species were found in extremely large numbers.

Serinya, Kaianja Island, Sesse Islands. (Masaka. 3,500.)

19.v.54. No larvae of Trichoptera collected.

Sezibwa Falls. (Mengo. 4,000) and a fairly large stream flowing through thick, primary, montane forests about halfway between Jinja and Kampala.

25.v.54 and 4.vi.54. The stream cascades down some very steep falls about 100 feet high, widening out into a pool at the bottom. The vegetation is luxuriant and ferns are a marked feature. Trichoptera collected: Larvae of *Anisocentropus usambarensis* Ulmer and *Leptocerina ramosus pinheyi* Kimmins in abundance and larvae of two unidentified species.

Turtle pool, Mwiri. (Busoga. 4,000.)

29.v.54. Temporary pool on impervious laterite base. The dry mud may reach a temperature of over 40° C. during the dry season. The resident inhabitants include turtles, which seem to spend the dry season in fissures in the laterite, and "fairy-shrimps" (*Cheirocephalus*). No Trichoptera collected.

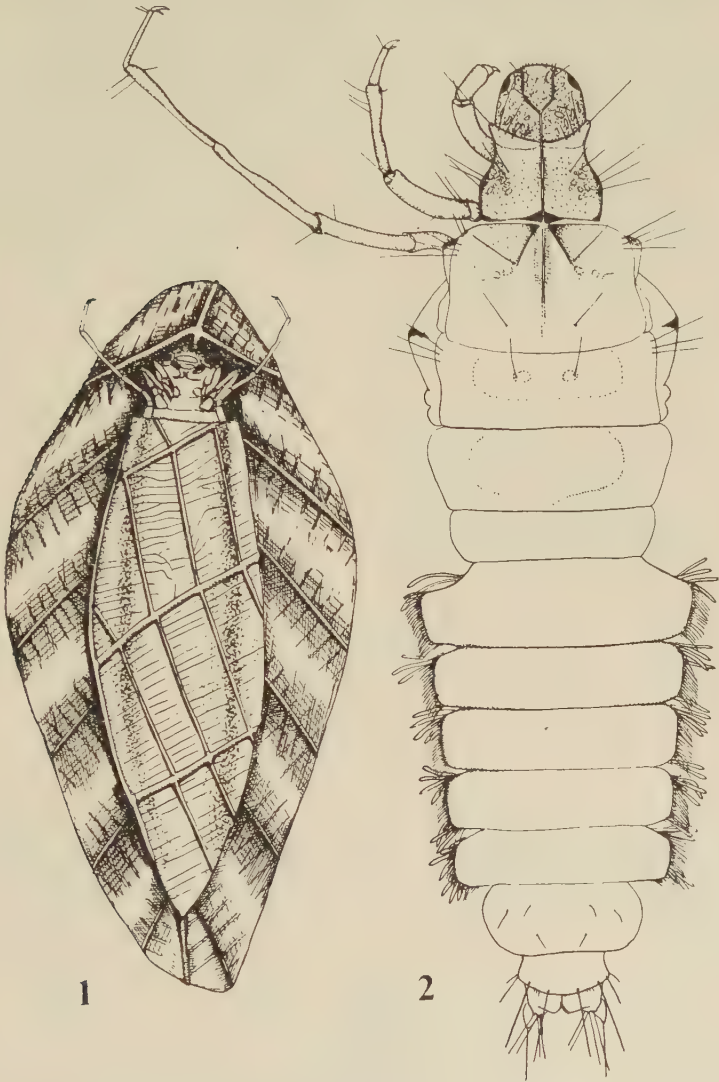
CALAMOCERATIDAE.

Anisocentropus usambarensis Ulmer.

A number of larvae was collected from the Sezibwa Falls, Uganda, on 25th May, and again on 4th June, 1954. They were particularly numerous close to the bank out of the main stream and were walking over the leaves fallen from overhanging trees. Adults emerged from aquaria at Jinja on 9th and 12th June and were identified by Mr. D. E. Kimmins.

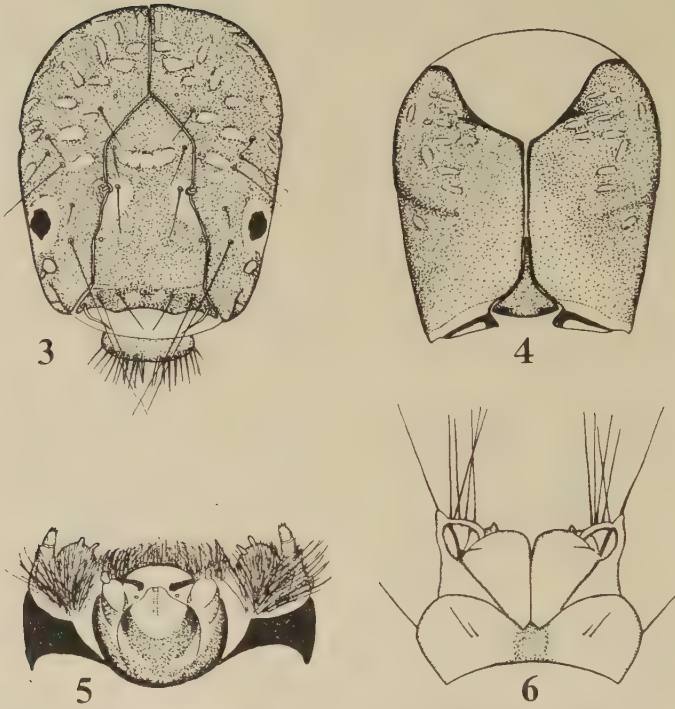
Case of two pieces cut from a leaf, the dorsally-disposed piece being the larger. The two sections are stuck together with a silk-like secretion and the smaller (ventral) has a keel-like projection which provides the space necessary to house the larva. Total length up to 37 mm., width 19 mm. A number of leaves found in the water, fallen from trees growing on the bank, had had the characteristically-shaped pieces cut from them by the larva. I am indebted to the Director, Royal Botanic Gardens, Kew, for identifying the tree as *Macaranga schweinfurthii* Pax. Larva strongly compressed dorsoventrally, widest at third abdominal segment; length 16.0 mm., width 4.5 mm. Gills present on second to eighth abdominal segments, filiform, joined together at their base. In the aquarium the larvae fed on the surface skin of leaves dropped into the water. Head dark golden-brown with yellowish muscle spots arranged in a characteristic pattern. Anterior margin of clypeus sinuate and dark in colour. Lateral margins of clypeus parallel aborally before they turn inwards to form the vertex. Clypeus mark transverse, lunate and made up of five muscle spots. Eyes situate in white

areas. Antennae small. A groove runs around the genae transversely in relation to the forward prolongation of the prothorax. The characteristic shape of the gular sclerite is shown in fig. 4. *Prothorax* light golden-brown and sclerotised, extending forwards to form a cup-like receptacle for the head capsule; lateral margins concave. Posterior margins



FIGS. 1-2.—*Anisocentropus usambarensis* Ulmer. (1) Larva in case from below. (2) Larva from above.

black and thickening considerably at the mid-suture. Prosternal horn absent. *Mesothorax* wider and longer than prothorax, with an ill-defined sclerotised area in anterior half. Two areas of heavy sclerotisation, black in colour, present at the centre of the anterior margin; here they are adjacent to the black areas on the posterior margin of the pronotum. *Meta-thorax* as wide as the mesothorax but not so long. No sclerotised areas present on the meta-



FIGS. 3-6.—*Anisocentropus usambarensis* Ulmer. (3) Head from above. (4) Head from below, mouthparts omitted. (5) Labium and maxillae from below. (6) Anal segment from below.



FIGS. 7-9.—*Anisocentropus usambarensis* Ulmer. (7) Right mandible. (8) Labrum from above. (9) Labrum from below.

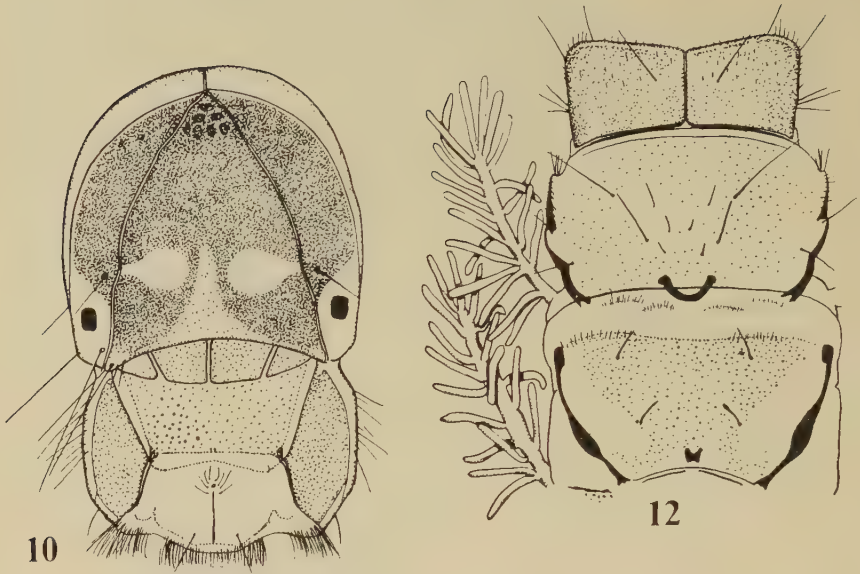
notum. Protuberances absent from the first abdominal segment but an ovoid platelike part on the metanotum probably represents the dorsal protuberance. A pair of lunate heavily-sclerotised plates present on the ventral surface. Abdomen creamy-white but the considerable gut contents showed through dark-brown. Second abdominal segment narrow but third segment wide with lateral wing-like extensions. (This segment is the widest of the body.) Fourth to seventh segments inclusive similar to the third segment but progressively narrower. Due to the lateral extensions the intersegmental grooves are deep. Eighth segment bulbous. A tufted lateral line present on third to seventh abdominal segments. *Labrum* rectangular with attachment sclerites black and hooked. About fifteen stout bristles on each side of the dorsal surface in a transverse band. *Mandibles* black, scoop-shaped, 4 or 5-toothed with a large tuft of golden hairs on inner faces of each. *Maxillae* and *Labium* obtuse, labium bulbous, base of maxilla black, palps very hairy at base. Labial palps of two segments, distal segment bearing a bristle, the proximal segment with sclerotised band having an inwardly-directed projection. *Legs* : Prothoracic legs short and deep. Pre-coxal sclerite hook-shaped and covered with short blunt spines. Mesothoracic legs longer than prothoracic but metathoracic legs exceptionally long, tibia about twice as long as femur and with a dilation, then a constriction, at about the mid-point. On all legs spinous bristles on ventral edge of femur absent, but very small spinous processes present. *Abdomen* : On each basal segment of the anal claw is a lappet surmounted by a long bristle. Claw small, bent inwards and with an auxilliary claw ; on the ventral surface a narrow sclerotised bar runs diagonally inwards to the posterior margin of the last abdominal segment. Hooked plate on each side of ventral surface of first abdominal segment.

HYDROPSYCHIDAE (MACRONEMATINAE).

Phanostoma senegalense Brauer.

Adults of this species occur in great numbers in the vicinity of the Ripon Falls where the Nile flows out from Lake Victoria. On the morning of 3rd May, 1954, the dead bodies of this species, together with those of a new species of *Cheumatopsyche* (U.5401), were about an inch deep around an electric light used to illuminate the Falls, and their decaying bodies gave off a peculiar sickly odour. The larvae are extremely common, inhabiting tough whitish-grey silk-like tubes underneath stones and boulders a few yards into the lake where the water has gathered rapid movement. A collection of larvae was made from the East Bank, but Dr. P. S. Corbet has since reported to me their presence on the West Bank also at this point. Larvae were also collected by me on the West Bank of the Nile about two miles downstream from the Owen Falls. About a dozen adults were reared in the laboratory at Jinja and identified by Mr. D. E. Kimmins.

Larva : Length 13 mm., width 3 mm., cylindrical. Dorsal surface light grey shading to dark grey with light brown areas. Ninth abdominal segment greenish. Ventral surface white, except last two abdominal segments. Intensity of coloration variable. This species is probably an important predator of *Simulium*. *Head* : Front of head bounded by false genal sutures, flat. Labium projecting slightly upwards to give front of head concave appearance. A wide dark brown to black area is bounded by a pair of false sutures in the genae enclosing and running roughly parallel to the lateral margins of the clypeus. Clypeus triangular with oral margin concave and two large white ovoid areas connecting with the lateral margins by a neck. Ventrally the genae along their oral margin are transverse and a series of small diminishing transverse concave folds extends aborally. A gular sclerite in its characteristic trichopterous form is absent. It may perhaps be represented by a narrow



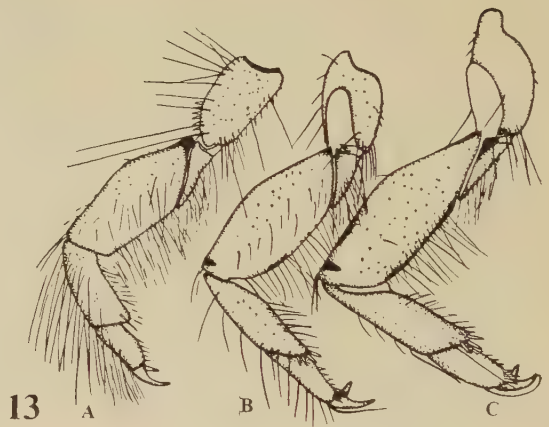
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13



14

FIGS. 10-14.—*Phanostoma senegalense* Brauer. (10) Head from above. (11) Head from below. (12) Thoracic nota. (13) Legs: A, prothoracic, B, mesothoracic, C, metathoracic. (14) Last abdominal segment from below.

transverse bar delimited at each side by a small round pit, and at the centre a triangular sclerotised plate, the apex anterior, covers the submental area of the labium. *Labrum* not sclerotised, somewhat prehensile and reminiscent of that of *Philopotamus* (Philopotamidae). Anterior margin convex and hairy, and wing-like lateral extensions hairy. *Mandibles* large, scoop-like, 4 or 5 teeth; outer margins hairy (as is general in Hydropsychidae). *Legs*: approximately equal, meso- and metathoracic legs only very slightly longer than prothoracic legs, light yellow. Tibia and tarsus of prothoracic legs and ventral edge of all legs very hairy. Ventral edge of tibia and tarsus of all legs beset with spines. Tip of distal hair of tarsus of metathoracic legs apposed to tip of tarsal claw. In all legs proximal segment of trochanter very small; except for hairs on the coxae, all hairs and bristles golden yellow. Tibiae of all legs rhomboidal, and a group of blade-like bristles at distal tip of ventral edge of meso-tibia and meta-tibia and tarsus.

SUMMARY.

Methods of collecting, transporting and rearing larvae of Trichoptera in tropical conditions are given. Larvae of *Anisocentropus usambarensis* Ulmer and *Phanostoma senegalense* Brauer from Uganda are described and figured.

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A NOTE ON THE STONEFLIES OF ICELAND.

By H. B. N. HYNES, Ph.D., F.R.E.S.

(Department of Zoology, University of Liverpool.)

WHILE preparing a key to the nymphs of the British species of *Capnia* (Hynes 1955), I examined some nymphs from the River Laxa, Myvatn, Iceland, collected by Miss Lucy Buxton in July, 1953, and very kindly presented to me. My observations led me to the conclusion that previous identifications had been erroneous. According to Tuxen (1938) the only species of stonefly known to occur in Iceland is *Capnia atra* Morton, and adults of this species have been recorded from the same locality as that from which my nymphs came. The species had been originally identified as *C. atra* by Dr. Bengtsson of Lund (Lindroth, 1931). On zoogeographical grounds this seemed reasonable, as *C. atra* occurs in the far north of Europe (Brinck and Wingstrand, 1949), and the very similar, if not identical, species *C. hantzschii* Ricker (1938) occurs in Baffin Land. These species are not, however, short-winged, and Tuxen states that all the Icelandic males seen by him had short wings.

I found that the nymphs did not resemble those of *C. atra* from Europe, but were very like those of *C. vidua* Klapálek, and further that the supra-anal lobe of the adult male, which was visible through the cuticle of two of the specimens, also resembled that of *C. vidua* and not that of *C. atra*. I am exceedingly grateful to Dr. S. L. Tuxen, of Copenhagen Zoological Museum, for the loan of an adult male from Iceland, which has enabled me to make a further study of this problem.

The genitalia of this specimen (fig. 1, B) show quite clearly that it is not *C. atra*, but that it closely resembles *C. vidua*. Fig. 1, A and C show details of the male genitalia of British specimens of *C. atra* and *C. vidua*. From these it can be seen that, apart from the very different shapes of the supra-anal processes, these species differ in the shape of the seventh abdominal tergum. In *C. vidua* this is deeply cleft posteriorly, and has a clearly defined membranous area mid-dorsally. In *C. atra* the sclerite is not cleft, and the membranous area is not clearly defined; indeed in some specimens it is difficult to see at all. In the Icelandic specimen the sclerite is even more deeply cleft than in British *C. vidua*. British *C. vidua* and *C. atra* males differ also in that the wings of the former extend only to the ends of the thoracic segments which bear them, whereas in the latter the wings extend to the end of the eighth abdominal segment.

Aubert (1950) has described three geographical races of *C. vidua* from the alpine region, north-west Europe and Britain, the males of which differ in the form of the supra-anal lobe, the degree of development of the spinose knob on the eighth tergum and the length of the wings. It would seem that the Icelandic specimen belongs to a fourth subspecies.

Tuxen (1938) has used the name f. *brachyptera* for Icelandic material and I propose that this form be named *Capnia vidua brachyptera* Tuxen.

The male differs from the other races as follows. Micropterous, but not so

markedly so as *C. v. anglica* Aubert, the forewings extending to the end of the metanotum and the hind wings to the end of the second abdominal segment. Spinose knob on eighth tergum even less protuberant than in *C. v. anglica*. Upper sclerite of supra-anal lobe as in *C. v. anglica*, lower sclerite more sharply and deeply incurved below. Tergum seven more deeply incised than in *C. v. anglica* and projecting upwards, as in *C. v. vidua* Klapálek.

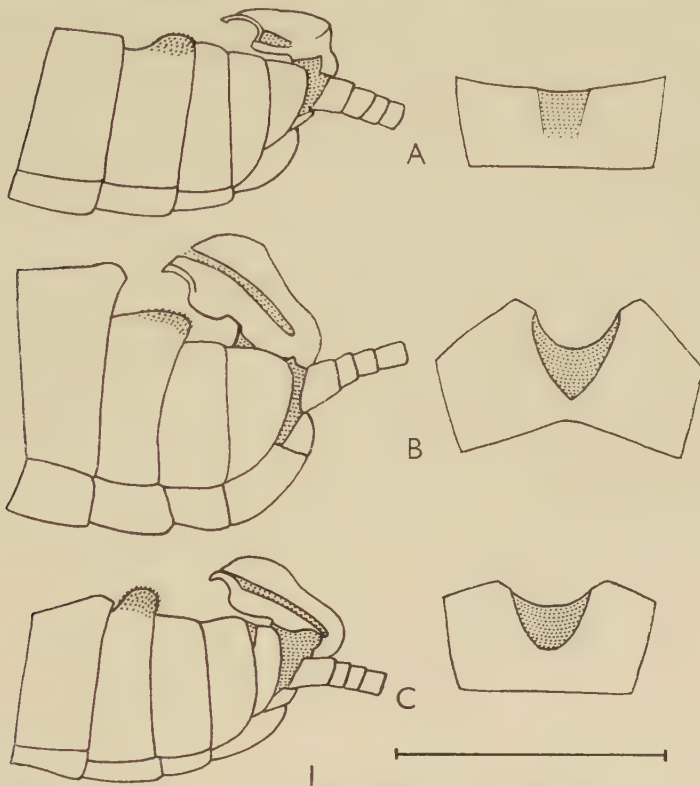


FIG. 1.—Tips of abdomen in side view and seventh abdominal terga in dorsal view of males of (A) *C. atra* from St. Mary's Loch, Selkirk, Scotland, 24th May, 1944, (*E. S. Brown*); (B) *C. vidua brachyptera* from Iceland; (C) *C. v. anglica* from Maize Beck, Teesdale, Yorkshire, 17th May, 1928, (*H. Whitehead*). Drawn with the aid of a projector. Membranous areas stippled. The line represents 1 mm.

I designate as holotype ♂, Varne, Kilde N. V. f. Ustifell, Skagali, Iceland (*Tuxen*) 14th April, 1937, in the collection of the Zoologiske Museum, Copenhagen.

The presence of *C. vidua* in Iceland is of considerable zoogeographical interest. As already stated, the presence of *C. atra* seemed reasonable, although one might have expected it to be accompanied by *Dirra bicaudata* (L.), which also occurs in the far north and is circumpolar (Hynes, 1952), as is apparently *C. atra* and its allies *C. hantzschii* and *C. nearctica* Banks (Ricker, 1944). *C. vidua*, on the other hand, has a far more limited distribution (Aubert, 1950), extending from the Alps to north-western and central Europe and England. It is appar-

ently absent from Scandinavia (Brinck, 1949) and Ireland (King and Halbert, 1910), and no closely allied species have been reported from North America. It presumably, therefore, has reached Iceland directly from the European mainland, or from England or Scotland, where it also occurs, and not via Ireland or Scandinavia. It may be noted here that no Plecoptera have been recorded from the Faroes or Greenland (Tuxen, 1938).

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A BIVALVE CAGE FOR SMALL ARTHROPODS.

By A. R. HILL, Ph.D., F.R.E.S.

(*Department of Zoology, Glasgow University*).

THE cage described here is intended for use in the study of small leaf-eating arthropods.

The two valves of the cage are sections, of convenient thickness, cut from perspex acrylic resin tubing of suitable diameter. The sections of tubing are carefully cut, preferably but not necessarily, on a milling machine, so that opposing surfaces are smooth or at least free from excessive unevenness. To one surface of each valve a lining of velvet is cemented. This lining ensures that the valves fit closely to the leaf. This is especially important where the lower valve is likely to traverse veins on the under-surface of the leaf and where very small arthropods are being studied.

The hinge joining the valves is simply constructed from a large safety pin from which the point and sheath have been removed. The cut arms of the pin are then crossed and bent as shown in fig. 1.

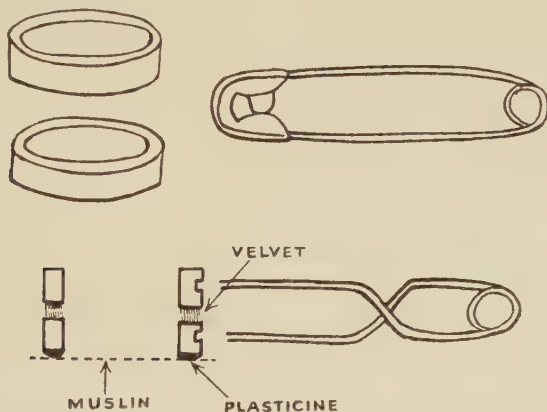


FIG. 1.—A bivalve cage for small Arthropods. (For explanation see text.)

The hinge is most conveniently secured to the valves by drilling one hole in each of the latter, of slightly narrower diameter than that of the pin. The valves are then held together with the holes one above the other; the cut ends of the pins are then heated and inserted into the holes. The perspex is thus fused by the hot wires and a very tight union is obtained.

A thin ring of plasticine is placed on the outer cut surface of one valve and a small square of muslin or similar material is pressed on to the plasticine to which it adheres firmly.

The complete cage is clipped on to a leaf and may, if necessary, be supported by means of fine wire or cord passed through the eye of the pin and fixed to a convenient twig of the food-plant or to a supporting cane, etc.

By lifting one corner of the muslin, insects, etc., may be introduced or observations made with great ease. Indeed, enough light penetrates to the interior of the cage to allow observations to be made without removing the cover. When the muslin is replaced it is pressed back on to the plasticine.

Although a slight smell can be detected from the plasticine, this has never been found to have any adverse effect on the insects enclosed in the cages.

BOOK NOTICES.

Dwellers in darkness : an introduction to the study of Termites. By S. H. SKAIFE. 8vo. London (Longmans Green & Co.), 1955. Pp. x + 134, pls., text illust. Price 25s.

In this work the author provides a fascinating picture of the life in colonies of termites, the most ancient of the social insects. He describes in detail the experiments carried out over twenty years, by means of which he has recorded their life and death, their direction, sustenance and activity.

The volume is well illustrated by numerous half-tone plates and line drawings.

Wings, insects, birds, men. By BLANCHE STILLSON. 8vo. London (Gollancz), 1955. Pp. 299, text illust. Price 16s.

This work is the result of the author's random studies instigated in the first place by an interest in the flight of birds and developing into a desire to know more about wings as organs of flight.

The work is in three Parts, of which Part I, comprising eight chapters, is devoted to Insects. These chapters are full of odd and fascinating information about the many forms and functions of wings—the vast range of variations between grasshoppers, dragonflies, locusts, beetles, bugs, butterflies; the varying processes of metamorphosis; the curiosities of the insects with sound-producing wings (including the varieties kept caged in China and Japan); the many other duties of wings—for air-conditioning the hive, as oars, as disguise, as an oxygen-tent to allow insects to submerge under water, and even as a means of hypnotising their prey.

Part II deals with birds and leads on to Part III, which deals with the principles of human flight.

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